A MATHEMATICAL CROP GROWTH MODEL FOR A MIXED STAND OF ITALIAN RYEGRASS (*Lolium multiflorum* L.) AND WHITE CLOVER (*Trifolium repens* L.)

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A Dissertation submitted to the Faculty of Science, University of the Witwatersrand, for the degree of Master of Science.

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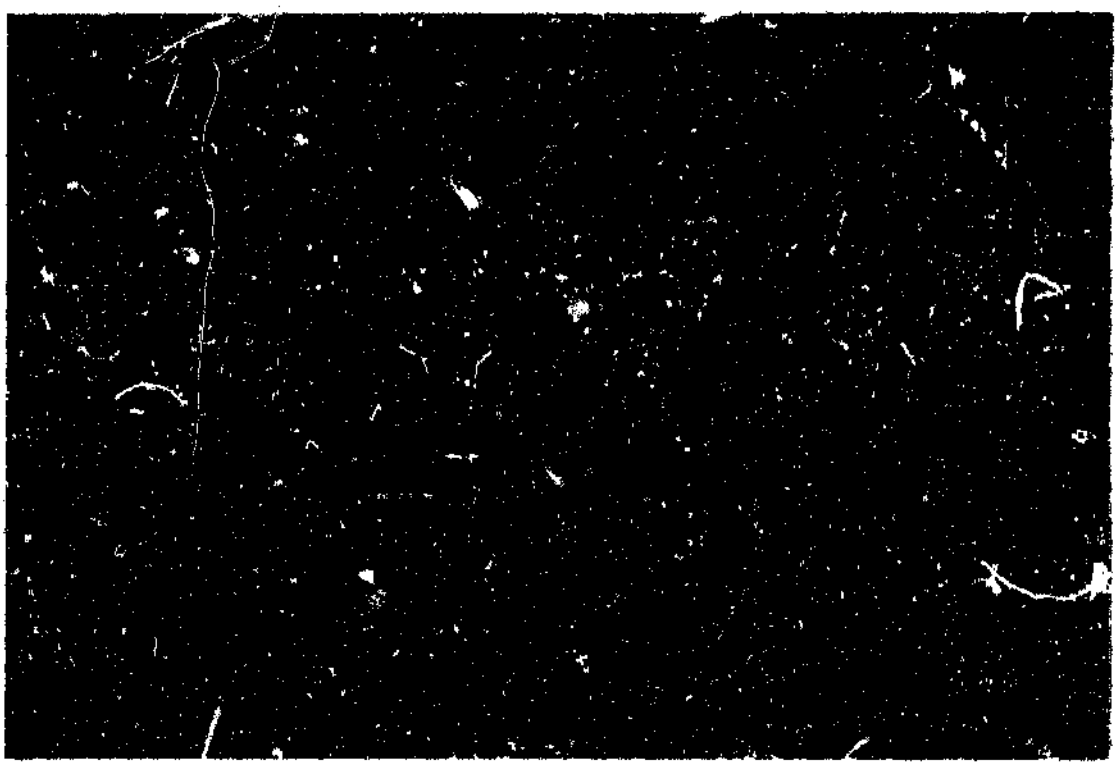

ABSTRACT

The main aim of this study was to develop a mathematical crop growth model for a mixed stand of ryegrass and clover. The modelling exercise consisted of an experimental component as well as the actual modelling component. The experimental part of the project was essential in terms of gaining a better understanding of the competitive interactions between ryegrass and clover, as well as being essential for obtaining all the necessary parameters and variables for the model.

The experimental results of the project revealed that although the single leaf photosynthetic rates of clover were higher than those of the ryegrass, the clover was outcompeted by the ryegrass in mixed swards. This was due to the better canopy structure and quantum yield efficiency of ryegrass relative to clover. It was also found that environmental temperature, and increasing levels of interspecific competition strongly influenced the growth rates and carbon allocation coefficients of these crops. The interspecific competition experiment showed that ryegrass benefitted from its interactions with clover, while clover was detrimentally affected. This experiment also indicated that a transfer of nitrogen occurred from the clover to the ryegrass.

The model was based on the assumption that the canopy structures and quantum yield efficiencies of the respective crops would largely influence their competitive abilities. The model was unique in that it was a mixed crop growth model which accounted for the environmental effects of fluctuating temperature and irradiance on photosynthetic rates. The model was found to simulate the growth of ryegrass and clover, both in monoculture and in mixture, to satisfaction.

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University, nor has it been prepared under the aegis or with the assistance of any other body or organization or person outside the University of the Witwatersrand, Johannesburg.

Date: 6 December 1992

Niki Papadopoulos

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I wish to thank the following people:

- My supervisor, Dr. V.M. Gray, for his enthusiasm, support, and invaluable assistance throughout the project. It was a pleasure working with such an approachable and friendly supervisor.

- My special friend and confidante, Monica Birkhead, who's confidence in me was an inspiration. Special thanks for all the excellent advice, encouragement, and assistance (both in the field and academically).

- Dr. M. Scholes for her valuable contributions during committee meetings.

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- The University of the Witwatersrand and the FRD for financial assistance.

- And last, but not least, my family for all their support and encouragement.

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LIST OF ABBREVIATIONS

α	quantum yield efficiency (gC/J)
Γ	CO_2 compensation point
δ	specific leaf area (m^2 leaf/g leaf)
Θ	conversion factor from carbon dioxide to carbon (dimensionless)
τ	leaf transmission coefficient
A	photosynthesis
A_c	canopy gross photosynthetic rate ($gC/m^2/s$)
Ac_1	canopy photosynthesis of ryegrass in mixed model ($gC/m^2/s$)
Ac_2	canopy photosynthesis of clover in mixed model ($gC/m^2/s$)
A_d	daily canopy photosynthetic rate ($gC/m^2/s$)
A_L	single leaf gross photosynthetic rate ($gC/m^2/s$)
Alphrf	α at optimum temperature
Amax	light saturated rate of photosynthesis ($gC/m^2/s$)
Amaxrf	Amax at optimum temperature
B	a constant in the Amax and α temperature dependence equations
b	a constant for the self-thinning rule
C	carbon
ppm	difference in CO_2 air streams before and after photosynthesis
CBM	conversion factor for converting g C to g biomass
CEC	cation exchange capacity
CO_2	carbon dioxide
D	the number of surviving plants
e	exponent
f_L	fractional C allocation coefficient to leaves
f_R	fractional C allocation coefficient to roots
f_S	fractional C allocation coefficient to stems
g	gram
h	canopy height (m)
I	intensity of radiation in the canopy after passage through a given leaf area ($J/m^2/s$)

I_L	irradiance incident on the surface of a leaf at depth L
Io	intensity of unintercepted radiation ($J/m^2/s$)
IRGA	infra-red gas analyser
J	Joules
k	canopy extinction coefficient (dimensionless)
$1 - k$	light penetration coefficient (dimensionless)
k_G	rate of storage C utilization ($gC/m^2/s$)
L	leaf dry biomass per unit ground area (g/m^2)
LA	leaf area per unit ground area (m^2)
LAI	leaf area index (m^2 leaf/m^2 ground)
LAI_1	leaf area index of ryegrass in mixed model (m^2 leaf/m^2 ground)
LAI_2	leaf area index of clover in mixed model (m^2 leaf/m^2 ground)
M	maintenance respiration rate (gC/gC/s)
m^2	meters squared
N:P:K	nitrogen:phosphorus:potassium
$N\text{-}NH_4$	ammonium nitrogen
NO_3^-	nitrate
O_2	oxygen
N	nitrogen
P	phosphorus
p	barometric pressure (kPa)
PFD	photon flux densit
R	root dry biomass (g/m^2)
Rg	growth respiration ($gC/m^2/s$)
R_L	instantaneous relative growth rate of leaves (g leaves/g plant/day)
R_R	instantaneous relative growth rate of roots (g roots/g plant/day)
R_S	instantaneous relative growth rate of stems (g stems/g plant/day)
Rs	rate of respiration ($gC/m^2/s$)
Rw	instantaneous relative growth rate of the whole plant (g/day)
s	second
S	stem dry biomass (g/m^2)

S.A.	South Africa
Sn	rate of senescence ($gC/m^2/day$)
T	temperature of environment (°C)
Tm	optimum temperature for photosynthesis (°C)
V	air flow rate through the leaf cuvette (cm^2/s)
VA	vesicular arbuscular
W	mean dry weight of plant (g/m^2)
Ws	storage carbon dry weight
WUE	water use efficiency
X	day of the year when harvesting started
XI	harvesting day of the year
XZ	factor for modifying α according to temperature
Y	yield efficiency (dimensionless)
Z	factor for modifying Amax according to temperature
°C	degrees Celcius

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INTRODUCTION

i) Introduction to the study

With the increasing cost of nitrogenous fertilizers, as well as the environmental implications associated with using fertilizers, there is growing interest in the possibility of greater use of grass-legume mixtures in forage crops. This is because of the ability of legumes to fix atmospheric nitrogen in association with *Rhizobium*, in their root nodules. The perennial ryegrass (*Lolium perenne L.*) - white clover (*Trifolium repens* L.) association is one of the more common such mixtures, particularly in New Zealand and the United Kingdom.

There are many advantages to growing white clover in association with pasture grasses. The major advantage of this association is that nitrogen is supplied to the grass component by the white clover, and so the potential exists to give good forage yields and sustain high animal production. Set against these advantages, however, is the problem that clover is usually at a competitive disadvantage compared to grasses and the success of this association depends on maintaining sufficiently large proportions of clover in the sward.

Several theories have been proposed to explain the poor competitive ability of clover relative to ryegrass. Some authors (Haynes, 1980; Dennis & Woledge, 1982) believe that the horizontal inclination of the clover foliage is a disadvantage in light interception when compared to the erect leaves of ryegrass. Others (Evans, 1977; Martin & Field, 1984) suggest that it is the better competitive ability of ryegrass roots which results in a faster initial growth rate of ryegrass, creating overtopping and shading of the clover by the ryegrass. It has also been reported (Davidson & Robson, 1986; Woledge et al., 1990) that clover has a slower growth rate than ryegrass at low temperatures which might explain the steady decline in the proportion of clover in mixed swards, particularly in temperate countries.

Whatever the reason/s for the poor competitive ability of clover relative to ryegrass, it is obvious that a better understanding is needed of the physiological processes underlying grass and clover competition. An understanding of the above and below ground competitive abilities of the respective crops with respect to competition for soil resources (nutrients and water) and

competition for light, is also needed. The factors determining how much light is intercepted by the leaves of each species, the relative leaf areas of the two crops, their photosynthetic rates and growth rates at different temperatures, and the heights they reach within the canopy, are but a few of the parameters that need to be investigated. Such knowledge can only be attained by carrying out the appropriate measurements of ryegrass and clover in the field, when grown in monocultures and in mixed swards.

More reliable methods of management will depend on a more comprehensive understanding of the competitive processes between ryegrass and clover. Furthermore, the development of a mathematical model describing the factors influencing the competitive interactions of these two species in mixtures will facilitate better management practises, resulting in much higher yields.

ii) **Objectives of the study**

1. To determine the effects of temperature on the growth rates, photosynthetic rates, and overall competitive abilities of ryegrass and clover, grown as monocultures and in mixture.

2. To establish whether the carbon allocation coefficients of ryegrass and clover are influenced by changes in temperature, changes in density, and changes in interspecific competition.

3. To determine the effects of sowing density on growth and overall competitive abilities of ryegrass and clover.

4. To determine whether there is any benefit to either/both crop(s) when grown together in

5. [illegible]thematical model, using data from experiments, to simulate the growth of ryegrass and clover with as monocultures and in mixture.

6. To validate the model by comparing model outputs with experimentally derived data.

CHAPTER 1

LITERATURE REVIEW

1.1. *Factors associated with the growth and competitive abilities of ryegrass and clover*

1.1.1. Temperature

Temperature is an important environmental factor influencing the growth rate of plants. The growth rate of a plant depends on its rate of photosynthesis, which is a chemical process involving the conversion of carbon dioxide into carbohydrates. This chemical process is catalysed by several enzymes which function optimally at a certain temperature.

The process of photosynthesis was mathematically defined by Rabinowitch (1951), and this mathematical description involves several photosynthetic parameters. These include Amax, the rate of gross photosynthesis at saturating irradiance levels; Θ, a dimensionless parameter which is a conversion factor from carbon dioxide to carbon; and α, the quantum yield efficiency which is obtained from the initial slope of the response of gross photosynthesis to changing irradiance levels incident on the leaf. The quantum yield efficiency is also reflected by the ratio of carboxylase to oxygenase activity of rubisco (Ehleringer & Pearcy, 1983). Amax and α have been found to be dependent on temperature. Johnson and Thornley (1984) found that Amax depended strongly on temperature for all plants, and α was found to decrease by about 14% over the range 14° to 24°C for C_3 plants but was independent of temperature for C_4 plants (Ehleringer & Björkman, 1977).

Other photosynthetic parameters defined by Charles-Edwards et al. (1986) are the CO_2 compensation point (Γ), which denotes the CO_2 concentration in the bulk air surrounding the leaf when the net rate of exchange of CO_2 between the leaf and the air is zero; and the carboxylation and oxygenation coefficients which are efficiency coefficients for CO_2 and O_2 utilization, respectively. The CO_2 compensation point (Charles-Edwards et al., 1986) and the quantum yield (Ehleringer & Björkman, 1977; Ehleringer & Pearce, 1983) were also reported to be highly dependent on temperature for several C_3 plants, and consequently the photosynthetic rates were strongly dependent on temperature. The only photosynthetic

parameter which appeared to be largely independent of temperature was Θ (Johnson & Thornley, 1985).

It is well known that high oxygen concentrations inhibit photosynthesis, and this phenomenon is called the oxygen effect. Jolliffe and Tregunna (1973) found that the O_2 effect was enhanced by higher temperatures, and that high CO_2 concentrations and low temperatures counteracted the inhibitory effect of O_2.

The response of quantum yield to temperature was investigated by Leverenz and Oquist (1987) and it was suggested that several factors were responsible for this response. Among these was the well-described response of rubisco oxygenase and carboxylase activity to temperature. Differences in stomatal conductance between or within species could also affect quantum yield through rubisco activity. They also suggested that membrane properties may change with temperature, affecting leakage of protons out of the thylakoids, and a reduced efficiency of photophosphorylation could also reduce quantum yields.

From the above discussion it is clear that temperature has a marked effect on the photosynthetic capacity, and consequently the potential growth rates, of plants. Thus, if photosynthesis is temperature dependant, and the rate of photosynthesis determines the growth rate of a plant, it is reasonable to assume that the growth rate of plants should vary seasonally.

Many authors have examined the temperature effects on the growth and competitive abilities of ryegrass and clover, both in monocultures and in mixed swards. The rates of net photosynthesis of leaves of both ryegrass and clover were found to increase substantially as the temperature was increased from 3° to 25°C under a constant water vapour saturation deficit (Woledge & Dennis, 1982). There was a general consensus that the competitive ability of clover was very poor at low temperatures relative to that of ryegrass, and that the amount of dry weight present in clover was much less than in ryegrass (Woledge, 1972; Woledge & Dennis, 1982; Davidson et al., 1986; Woledge et al., 1990). Woledge et al. (1990) found that the area, weight, number of live leaves per shoot, shoot density, leaf area index (LAI), and total above-ground weight were more adversely affected in clover than grass by the change from summer to winter. Davidson et al. (1986) suggested that this was probably due to a low rate of leaf expansion at low temperature (8-10°C) relative to that of perennial ryegrass. There

is evidence (Woledge, 1972; Davidson & Robson, 1986) that clover seedlings may not achieve maximum photosynthetic rates as quickly as ryegrass at low temperatures due to a lower leaf area production rate, resulting in ryegrass having three times more leaf area than clover during the early growth stages.

It was also reported that clover was at a poorer competitive ability during winter due to the change in canopy structure which resulted in clover being in a less favourable position than grass to intercept light during winter (Woledge et al., 1990).

The authors (loc.cit.) did not believe that the different growth rates of the respective plants during winter were attributable to differences in photosynthetic rates since little difference was found between the instantaneous rates of photosynthesis, of the two crops, at the same light intensity (Woledge & Dennis, 1982; Woledge et al., 1989; Woledge et al., 1990). Woledge and Parsons(1986) also found that there was no difference in the photosynthetic response to different temperatures by these crops when grown under different temperature regimes. Kessler et al., (1990) thought that there might be a temperature dependence of nodulation and nitrogenase activity which would result in poorer growth of white clover at low temperatures. However, after examining the effects of root and shoot temperature on nitrogen fixation and overall growth of white clover they found that temperature mostly limited growth independently of N fixation, even when root temperature was changed without a simultaneous change in shoot temperature. They concluded, from these findings, that N fixation plays only a minor role in the restricted growth of white clover at low temperatures.

At high temperatures clover was reported to have increased its proportion in a mixed grass/clover sward (Davidson & Robson, 1986). The shoot:root ratios, specific leaf area and leaf area expansion rate were all found to be higher for grass in mixture than monoculture suggesting adaptive responses to stress, resulting from shading, which was particularly noticeable at high temperatures when clover had a high positive aggressivity (Davidson & Robson, 1986).

Other findings of the seasonal effects of temperature included its effects on the overall characteristic growth pattern of mixed swards. The leaves of clover were found to be nearer the base of the canopy than those of the grass, resulting in a lower rate of photosynthesis in

situ in the canopy (Woledge, 1988). This author further observed that the tendency of clover to have leaves in unfavourable positions in the canopy, for light interception, and to have a correspondingly lower rate of mean photosynthesis than its companion grass, was particularly predominant during the latter half of winter. This was in contrast to the situation in summer when clover leaves were held high, resulting in a concentration of the leaf area in the upper portion of the canopy (Woledge, 1988).

1.1.2. Photosynthetic capacity and light interception

Given the fact that clover is a poor competitor, relative to ryegrass, in a mixed ryegrass/clover sward (Woledge & Dennis, 1982; Davidson *et al.*,1986; Woledge *et al.*, 1990), it could be assumed that clover has a lower photosynthetic capacity than ryegrass. This was, however, found not to be the case since the rates of photosynthesis of individual leaves of ryegrass and clover were found to be similar, if not higher for clover, at temperatures between 5° and 25° C, when leaf area and irradiance were equal (Dennis & Woledge, 1982; Woledge, 1986 and 1988; Woledge *et al.*, 1990). Although the photosynthetic capacity of individual clover leaves is at least as high as that of ryegrass, data of the *in situ* photosynthesis in the canopy suggests that grass swards have higher photosynthetic rates than clover swards (Woledge *et al.*, 1989). The reason for this finding is that canopy photosynthesis depends not only on the photosynthetic capacity of the individual leaves within a canopy, but also on the distribution of the leaf angles, which in turn determines how light is distributed among the leaves making up the canopy. The efficiency of light interception by a plant and the distribution of light within a canopy are determined by the orientation, position, shape and size of the leaves; i.e. the canopy stucture (Campbell & Norman, 1989). For example, in an erect crop, such as ryegrass, light penetrates more deeply into the canopy and hence is more efficiently used than in a crop with horizontal leaves, such as clover, in which the upper leaves may be light saturated while the lower ones are shaded. Dennis & Woledge (1982) concluded that the rate of dry matter production and the ceiling yield of clover were limited by the structure of the canopy rather than because of an intrinsically low photosynthetic capacity of individual leaves. Monsi and Saeki (1953) were amongst the first to develop quantitative methods to investigate the relationship between canopy structure and the penetration of light. They proposed a mathematical model to describe the vertical attenuation of light through cumulative layers of

leaves making up the canopy. This lead to an exponential relationship analogous to the Beer-Lambert law:

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

where I_o is the intensity of vertically projected incident radiation, I is the intensity of radiation after passage through a given leaf area index (LAI), and k is a constant, the canopy extinction coefficient. The canopy extinction coefficient gives a measure of the degree of light penetration into a canopy and is a function of the leaf orientation and leaf inclination (Newton & Blackman, 1970; Campbell & Norman, 1989). Horizontal leaves (eg. white clover) have canopy extinction coefficients approaching 1, therefore light does not penetrate far into the canopy, whereas plants with erect leaves (eg. ryegrass) have canopy extinction coefficients approaching zero, therefore light penetrates deeply into the canopy.

Other factors that were found to affect the canopy photosynthetic capacity, besides canopy structure, were the stage of growth and temperature. In ryegrass, the rate of photosynthesis of individual leaves was high during the early stages of growth in the field, when the foliage was sparse (Woledge & Leafe, 1976; Woledge, 1977). As growth proceeded in vegetative swards the photosynthetic capacity of successively expanded leaves fell progressively to almost half, due to increased shading which was a result of tillers and increased plant density. When the ryegrass plants were in the reproductive phase, however, the photosynthetic capacity of successively expanded leaves did not fall. The cause of the difference between vegetative and reproductive swards was believed to lie in their structure (Woledge & Leafe, 1976). In vegetative swards the stem apex was found to remain near the soil surface and new leaves developed in the shade of older leaves resulting in reduced photosynthetic capacity. In reproductive plants, the elongation of the stem carried the apex and expanding leaves high in the sward where they developed in full sunlight and so had a higher photosynthetic capacity. The rates of photosynthesis of newly expanded white clover leaves from the mixed sward were similar to rates found in ryegrass leaves at the beginning of the growth period (Dennis & Woledge, 1982). But, unlike vegetative ryegrass swards where there was a marked decline in photosynthetic capacity of successive newly expanded leaves as sward leaf area increased, the photosynthetic capacity of newly expanded clover leaves fell by only 20% initially and then not at all (Dennis & Woledge, 1982). This finding might indicate adaptation to shading.

Woledge (1986) observed that the changes in photosynthetic rate of white clover leaves with age were very similar to those reported for ryegrass, and that in this respect clover was not at an inherent disadvantage compared with ryegrass. Furthermore, it has been reported that through rapid petiole elongation the clover was able to position a greater proportion of its leaves near the top of the canopy, thus creating maximum photosynthetic capacity by avoiding shading effects on developing leaves (Dennis & Woledge, 1982; Woledge, 1986; Schwank et al., 1986). But, although clover produces leaves of a high photosynthetic capacity, they form a horizontal surface near the top of the sward thereby making less efficient use of the light than a pure grass sward, which due to its vertically inclined leaves allows light to be more evenly distributed through the canopy. Consequently, clover canopy photosynthesis appears to be less than that of grass (Dennis & Woledge, 1982).
Woledge et al., (1989) found that during winter clover had a lower rate of photosynthesis than the grass in situ in the canopy. This was because the clover leaves were nearer the base of the canopy than those of grass. In summer the situation was reversed, with clover leaves having a greater rate of photosynthesis in situ than grass, and the clover leaves were predominantly near the top of high LAI canopies (Woledge, 1988; Woledge et al., 1989).

Temperature also affects the photosynthetic capacity and light interception ability of the crops. Woledge and Parsons (1986) found that the rate of gross canopy photosynthesis of ryegrass, in bright light, increased with increasing temperature up to at least 20°C. Other authors, for example Sheehy (1977), reported little increase in canopy photosynthesis with rising temperature. This discrepancy was suggested to be due to differences in the water vapour saturation deficit (Woledge & Parsons, 1986). Those authors that did not observe an increase in canopy photosynthesis with increasing temperature appear not to have maintained a constant water vapour saturation deficit so that any effect of temperature may have been offset by the effects of increasing saturation deficit. This is most likely to be the case in the natural environment thus restricting photosynthesis of crop canopies.

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1.1.3. Competition for resources

Individuals living within the same community will be exposed to competition from like and unlike individuals when the demand for an essential resource exceeds its immediate supply (Haynes, 1980; Hill & Michaelson-Yeates, 1988). The resources for which plants are likely to compete are water, nutrients such as nitrogen and phosphorus, oxygen, carbon dioxide, and light. Tilman (1984) showed that in a wide array of terrestrial habitats, soil resources, especially nitrogen, water, phosphorus, potassium, magnesium, and various trace metals limited plant growth. Light availability at the soil surface for seedlings and new shoots is also an important limiting resource (Björkman & Ludlow, 1972). Other factors reported to influence the competition of two species are population sizes (Keddy, 1989), morphological and physiological differences (Givnish, 1982; Gutshcick, 1987), and resource partitioning (Tilman, 1982; 1985).

It is important to note that competitive differences are not necessarily reducible to a single factor, since these different factors are interrelated and they interact in a complex manner and in different ways under different situations (Haynes, 1980). Furthermore, it must be kept in mind that both intra- and interspecific competition are occurring simultaneously within a mixed community. Experimental evidence indicates, however, that intraspecific competition is often more intense than interspecific competition because similar individuals make comparable demands upon these resources (Connell, 1983; Hill & Michaelson-Yeates, 1988). This was apparent when analysis of the competitive interactions among a set of white clover and perennial ryegrass populations indicated that intraspecific pressures exerted by the white clover plants upon themselves were significantly greater than the interspecific pressures they exerted upon the ryegrass (Hill & Michaelson-Yeates, 1988).

Plants have been reported to be capable of adjusting the supply and demand of resources (Bloom et al., 1985; Gutschick, 1987). They adjust supply by increasing allocation of internal reserves to the acquisition of scarce resources and adjust demands by varying storage and growth patterns (Bloom et al., 1985). To acquire more of a soil resource, a plant must allocate its potential growth to below-ground structures for nutrient uptake, but to acquire more light, a plant must allocate its growth to above-ground photosynthetic structures (Tilman, 1982;

1985; Gutschick, 1987). Thus, individual plants face a 'trade-off' in their competitive abilities for a limiting soil resource versus light (Orians & Solbrig, 1977). Because N (or any other soil resource) and light are essential resources, foraging theory (Tilman, 1982) predicts that the optimal pattern of allocation to meet these conflicting resource requirements is the pattern that leads a plant to be equally limited by both.

Under resource limiting conditions the supply of a limited resource may result in the inability to acquire another resource. For example, supplies of C and water are often inversely related. Precipitation supplements the water supply, but reduces the photon flux density (PFD); i.e. the C supply. Conversely, conditions associated with high PFD typically increase evaporation and transpiration, thereby decreasing water availability in the soil (Bloom et al., 1985). In contrast, the demand for CO_2 and water are correlated. Stomatal aperture concomitantly controls CO_2 diffusion into and water loss out of a leaf so that high CO_2 demand entails high water demand. Growth, and consequently C demand are reduced under water stress by stomatal limitations to photosynthesis and by lack of adequate turgor for cell expansion.

Resource acquisition and optimal allocation are extremely sensitive to environmental variation (Bloom et al., 1985). On a very poor soil, total biomass would be low, causing little attenuation of light. A plant that allocated more of its potential growth to below-ground structures for resource acquisition would be favoured over a plant that allocated more to above-ground photosynthetic structures, because the former would acquire more of the limiting resource and thus reproduce more rapidly (Orians & Solbrig, 1977). In contrast, in a habitat with a nutrient-rich soil, high plant biomass would be produced, causing significant attenuation of light. This would favour an individual that allocated more of its potential growth to above-ground structures for efficient light use; i.e. a higher shoot: root ratio (Grimes & Hunt, 1975).

The architecture of a leaf canopy is fundamental to light interception by plants (Haynes, 1980). A critical characteristic of a plant in a light-limiting habitat is its height. Because light tends to be a directional resource, taller plants intercept more light (Givnish, 1982). Trenbath (1974) also concluded that in a mixture, the component with its leaf area higher in the canopy is at a general advantage. In most cases in grass-legume pastures the grasses are taller and more vigorously growing plants than the legumes, and this often leads to shading of the legumes. The angles of leaves to the horizontal and the area of the leaves are also important

adjuncts to canopy height in determining the competitive ability of plants for light (Haynes, 1980). The degree of attenuation of light within a plant canopy is largely determined by the amount of foliage present (this is usually expressed in terms of LAI), and the canopy extinction coefficient (k), which is an expression of the angle of the leaves to the horizontal. In plants with flat horizontal leaves such as clover, a high LAI is a disadvantage because of excessive self-shading. In grasses, however, which have vertically inclined leaves the light is distributed more evenly throughout the leaf canopy and consequently k is low (± 0.25) (Loomis & Williams, 1969).

The shoot and root growth rates and morphologies of two species growing together in a mixed sward also influence the competitive abilities of the respective plants in the mixture. White clover grows as a plagiotropic shoot system (stoloniferous), rooting at the nodes, while grasses have a typical 'phalanx' form, with closely packed tillers and little lateral spread (Thompson & Harper, 1988). The growth habit of clover ensures that the plants continually meander through the patchwork of associated grasses resulting in individual genets of clover, as they extend and branch in a sward, experiencing a range of environments from open, well illuminated gaps, to deep shade under the canopies of grass plants. The growth of clover in a grassland sward is promoted by close grazing or harvesting and reduced by treatments that favour the growth of grasses. This effect is usually ascribed to competition between the grasses and clover for limiting resources below-ground or to competition in the canopy for light (Davies & Evans, 1983).

Martin and Field (1984) examined the effects of shoot and root competition of perennial ryegrass and white clover. The plants were grown in boxes which were divided into compartments which separated either the roots, or shoots, or both (see Snaydon, 1979), so that shoot and root competition could be studied independently, or together. Perennial ryegrass was found to be the more competitive species in the study due to the combined effects of its more aggressive root and shoot systems. During the early stages of growth the ryegrass had a greater root competitive ability, which Evans (1977) attributed to its faster growing, longer, and more finely branched root system, enabling it to exploit nutrients in advance of the white clover. This greater root competitive ability of ryegrass during the early stages of growth, consequently led to greater growth of above-ground parts which resulted in a greater shoot

competitive ability of ryegrass over clover. The resultant effect on the clover was reduced growth due to shading by the ryegrass.

It has also been observed that the shading of the clover, by the ryegrass, influences the growth pattern of the clover (Solangaarichichi & Harper, 1987; Thompson & Harper, 1988). Thompson and Harper (1988) grew plants of white clover under simulated canopies of detached ryegrass leaves floating on tanks of water, and adjusted the density so that the intensity of photosythetically active radiation (PAR) was the same as under the real leaves. When the clover plants were allowed to grow from an open, exposed environment into the neighbourhood of grasses they ceased to branch actively and growth became largely confined to the linear extension of the main axes. Also, there was greater elongation of petioles under grass canopies with the shortening of internodes; i.e. the ratio of petiole length to internode length was increased dramatically under the grass canopies. The development of longer petioles, made possible by a sacrifice of resources to branching and internode elongation, was the only way by which clover laminae could be carried to the top of the sward, in an attempt to improve clover shoot competition for light.

Physiological differences between plants also affect their ability to compete for resources. The quantum yield efficiency determines the efficiency with which a plant utilises low levels of irradiance. Grasses have been reported to adapt more readily to shaded conditions and are less affected by reduced light intensities than clovers (Langer, 1973).

The water use efficiency (WUE) of a plant is an indication of the ability of a plant to control water loss under conditions of water stress. Clover was reported to have poor control of leaf transpiration resulting in low leaf water potentials and increased leaf senescence (Burch & Johns, 1978).

The root cation exchange capacity (CEC) of legumes was reported to be ± twice that of grasses (Volz & Jacobson, 1977). This suggests that legumes are poor competitors for potassium when grown in association with grasses.

Competition and other interferences between plants also play an integral role in the ecological principle of succession in which assemblages of species succeed one another until a steady state is reached (Haynes, 1980). Tilman (1982) developed a simple model of succession, the

resource-ratio hypothesis. The resource-ratio hypothesis was based on the assumption that the process of species replacement depends on plants' competitive abilities for resources. In other words, plant species are specialized on different proportions of limiting resources and the composition of a plant community should change whenever the relative availability of the limiting resources changes. If species are differentiated in their responses to limiting resources, and if the proportions of these resources change through time, then succession will result. Competitive ability for light, often referred to as the degree of shade tolerance, is also cited as a determinant of species replacement (Tilman, 1985).

1.1.4. Nitrogen application

The application of nitrogenous fertilizer has been isolated as one of the factors affecting the growth and competitive ability of ryegrass and clover in mixed swards (Marti & Field, 1984; Dennis & Woledge, 1985; Davidson & Robson, 1985 and 1986; Davidson et al., 1986). Although the present study was not concerned with the effects of nitrogenous fertilizer application to the respective crops, the results of other such studies will be briefly discussed to give a better overall understanding of the crops.

The application of nitrogenous fertilizer to a mixed sward of ryegrass and clover caused an increase in the growth of the grass while the clover growth was depressed (Dennis & Woledge, 1985; Davidson et al., 1986; Woledge, 1988). This was particularly evident at low temperatures (Davidson & Robson, 1986). The clover was, however, seen to grow at a much higher relative growth rate than the grass when nitrogen was not applied to the mixed sward, especially at high temperatures (Davidson & Robson, 1986).

Studies of nitrogen application to monocultures of ryegrass and clover showed that for the high-N ryegrass monocultures the total dry matter yields exceeded those for high or low N clover monocultures, and the difference was much more marked in mixtures than in monocultures (Davidson & Robson, 1986; 1990). There was, however, no significant difference between the dry weight of clover plants in monoculture or mixture (Davidson & Robson, 1990). These differences in yield should reflect differences in total photosynthesis, but it was observed that there was no difference in the photosynthetic rates of either ryegrass or clover between the N treatments (Dennis & Woledge, 1985; Davidson & Robson, 1986).

It was also observed that grass plants in mixture had significantly more tillers than those in monocultures (Wilman & Asiegbu, 1982; Davidson & Robson, 1990), while there was no difference in stolon growing point number between clover in monoculture and mixture (Davidson & Robson, 1990). Nitrogen application to clover monocultures showed no effect of N on yield (Dennis & Woledge, 1985), suggesting that the adverse effect of N on clover in a mixture appears to be due to an increased growth rate of the grass, causing shading of the clover and subsequently reducing the amount of carbon being fixed by the clover (Haynes, 1980). This suggestion was supported by Davidson and Robson (1990) who found that grass in mixture had consistently higher specific leaf areas than that in monoculture, indicating that competition for light, rather than for N, was the cause of clover decline relative to ryegrass. An increase in ryegrass canopy height and leaf size, when N was applied, were reported by Wilman and Asiegbu (1982). Laidlaw and Steen (1989) also showed that the effects of N on production of swards were principally due to increased tiller density in ryegrass, although faster leaf extension rate also seemed to be implicated. The authors (loc.cit.) concluded that the adverse effect of N on clover was due to the inhibition of branching rather than the reduction of stolon production. Davidson & Robson (1985) suggested that the better growth of grass in the high N treatment was probably largely due to the investment and retention of a greater proportion of the available carbon in the leaves, at the expense of investment in the roots.

Nitrogen treatment was further found to have a large effect on the dry matter partitioning of the grass. In the low-N grass plants there was a marked shift in dry matter partitioning towards the roots (Davidson & Robson, 1985; Davidson et al., 1986). In high-N grass the reverse was observed, with a greater proportion of dry weight being partitioned to the lamina and sheath, with a decrease in root length (Martin & Field, 1984; Davidson et al.,1986). The effects of N treatment were less pronounced in clover, the only noticeable change being that nodules comprised about twice the proportion of dry weight in the low-N compared with the high-N treatment (Davidson et al., 1986). Wilman and Asiegbu (1982) found that the application of N to clover reduced stolon diameter, increased petiole length and had little or no effect on leaf weight. These authors concluded that the petioles may have grown longer in response to the taller grass, and subsequent increased shading, rather than in direct response

to the applied N.

Some discrepancy exists in the literature as to whether there is a transfer of fixed N from the clover to the ryegrass in mixed swards. Whitehead (1970) suggested that the majority of transfer occured via the grazing animal and its deposition of dung and urine, or through decomposition of dead root and nodule tissue. This was supported by Ledgard (1991) who found that a significant amount of excreta N (particularly dung N) was incorporated into the soil and mineralised over time. Davidson & Robson (1985) claimed to have found no detectable transfer of fixed N from clover to ryegrass, but in a later paper (Davidson & Robson, 1986) they reported that N contents were at minimal levels in all the low-N grass plants, but were consistently higher in mixture than in monoculture. Evans et al. (1989) also found that coexisting mixtures yielded more grass in spring, which they thought was probably reinforced by the N transfer process between clover and ryegrass. Ledgard (1991) reported that 50% of grass N was met by transfer of fixed N from white clover, and that the below-ground N transfer was largest during dry summer conditions.

The ^{15}N isotope dilution technique is a popular method for estimating N transfer under field conditions (Barea et al., 1989; McNeil & Wood, 1990; Morris et al., 1990). The method works on the assumption that grass benefits from N transfer if it possesses a lower $^{15}N/^{14}N$ ratio when growing mixed with the legume than when growing alone, since this would suggest that the ryegrass absorbs more N that is fixed by the clover (^{14}N) than free N from the soil (^{15}N). Barea et al. (1989) found evidence of N transfer from clover to ryegrass, as indicated by the atomic composition of the grass. The concentration of N in the shoots of the grass was higher when it grew in mixture than when alone. This indicated an obvious benefit of intercropping, but the authors suggested that it could be merely due to better competition for soil N, so that the grass interplanted with clover would be less N limited than when grown alone. McNeil and Wood (1990) also found that there was a major dry matter benefit to the grass in the mixture, and they showed that the grass in the mixture received fixed N from the clover. In another study, Menchaca & Connolly (1990) found that in a low nutrient environment the rate of growth of ryegrass rapidly decreased, as did its relative influence on clover, which favoured an increment in the rate of growth of clover. This decline in ryegrass yield per individual

continued over harvests in the pure stands, but in mixture it was arrested after two months. In the last two harvests of the experiment it was seen that increasing density of clover had an enhancing effect on the yield of ryegrass. The availability of increasing quantities of clover-fixed N provides a reasonable explanation for the later harvest increases in ryegrass.
Although most authors agree that there is a transfer of fixed N from the clover to the ryegrass, there is still uncertainty as to whether this is a direct or an indirect transfer of N via mineralisation of senescing clover roots or nodules.

1.1.5. Density and self-thinning

The self-thinning rule of plant ecology states that as communities of plants mature, increases in the mass of above-ground plant material per unit area tend to be accompanied by decreases in the number of plants per unit area (Hardwick, 1987). Westoby (1984) defines the self-thinning rule as the mortality imposed by a plant on itself. The self-thinning rule can also be expressed as follows Lonsdale and Watkinson (1983):

$$W = bD^{-3/2}$$

where W = the mean dry weight per plant of the survivors

D = the number of surviving plants and their level of performance in terms of surviving stand density

b = a constant

The above equation defines a straight 'thinning line' of slope -3/2 (Westoby, 1984).
It is generally accepted that most plants fit the curve of self-thinning, but Lonsdale and Watkinson (1983) observed that there had previously been little attention focussed on the biological significance of the constant, b. They argued that the restriction of b to a relatively narrow range of values suggested that plants did not differ widely in their ability to utilize space when undergoing self-thinning. Based on this argument Lonsdale and Watkinson (1983) investigated the effect of plant geometry on the self-thinning line of perennial ryegrass. They found that plant morphology and canopy architecture affected not only the biomass which could be packed into a given volume but also the pattern of light attenuation through the canopy. White (1980) also showed that canopy structure influenced the intercept of the thinning line, and coniferous trees generally had higher intercepts than deciduous trees while

grasses had higher intercepts than dicotyledons. Presumably the narrow, erect leaves of grasses and the pyramidal profile of conifers improved the efficiency of light interception and allowed closer packing of plant material into a given volume of space, or the development of a greater stand height, before thinning commenced.

If it is lack of light that results in the mortality of suppressed individuals during self-thinning then the pattern of light attenuation in populations of grasses would allow a greater stand height to develop, than in the case of horizontal leaved clover plants, before the light flux is reduced to a value which results in the death of individuals in the lower regions of the canopy.

Lonsdale and Watkinson (1982) studied the effects of high sowing density on perennial ryegrass monocultures. They found that there was an increase in shoot:root ratios at higher densities and that shoot:root ratios were generally higher in shaded than in unshaded populations. The progression towards 'shootiness' was thought to be a consequence of greater mutual and self-shading as thinning proceeded. Population numbers declined from the initial sowing densities not only as a result of self-thinning, but also as a result of negatively density-dependent seed germination. For example, at a sowing density of 300 000 seeds.m^{-2} only 45% of the seeds germinated, in comparison with 95% at 1000 seeds.m^{-2}.

1.1.6. Defoliation by grazing or harvesting

Considering that ryegrass and clover are pasture crops their survival would depend on an adaptation mechanism which would ensure rapid recovery after defoliation. The success of such a re-establishment mechanism could play a major role in influencing the respective competitive abilities of the crops. Much work has been done to ascertain the responses of perennial ryegrass and clover to defoliation.

Chen and Wang (1988) conducted a theoretical analysis of the potential productivity of ryegrass under grazing and concluded that the potential productivity under grazing was higher than that under infrequent grazing. Martin and Field (1984) observed that following defoliation, during regrowth, perennial ryegrass had a greater rate of growth and a higher canopy of upright leaves within which light was well distributed, than clover. Perennial ryegrass thus acquired a greater competitive ability for light over white clover, which had a comparatively slower growth rate and horizontally inclined leaves.

The N re-mobilization during ryegrass re-growth was studied by Ourry et al. (1988) as a function of time, by labelling root and stubble compounds with ^{15}N before harvesting. The results showed that ryegrass re-growth involved two periods of differing physiological significance. The first occurred during the first 6 days after harvesting when nearly all the N supply for re-growth appeared to be highly dependent on organic N reserves from roots and stubble. Translocation of free amino acids and products of protein degradation provided the major source of N, whereas uptake and reduction of NO_3^- remained at a low level, demonstrating the inabilty of the plant to reduce NO_3^- when new leaves were not yet formed. The second phase (after day 6) was more representative of the stable behaviour of ryegrass, with assimilation of mineral N from the soil medium providing the predominant source of N for re-growth.

Although it was generally agreed that grazing increased the productivity of ryegrass, a review of the literature revealed some discrepancies regarding the effects of grazing on clover. Haynes (1980) stated that both ryegrass and clover were well adapted to being pasture crops. Grasses have shoot meristems which lie close to the soil surface, well below the level normally reached by the grazing animal, and both tillers and expanding leaf blades are able to continue growth after defoliation. Stoloniferous legumes, such as white clover, were also reported by this author to be well adapted to grazing due to their prostrate habit enabling rapid recovery from cutting or grazing. It was also found (Chapman et al., 1991) that in white clover, after defoliation, there was an increase in the rate of photosynthesis and an increase in the % export which boosted the amount of available carbon, to support affected sinks. Total root weight also declined following defoliation, and some mobilization of previously-stored material may have contributed to this difference. The authors found no evidence to suggest that white clover was any less well-adapted physiologically than its common grass companions to defoliation patterns typical of grazed pastures, since the nature of assimilate distribution and the rapidity and magnitude of physiological responses to defoliation suggest that white clover has a high degree of physiological integrity and plasticity. Woledge (1988) also found that clover had higher photosynthetic rates in situ in the mixed sward after defoliation, than the ryegrass. Woledge (1988) suggested that the reason for clover being found in progressively reduced proportions in mixtures over time was because clover has a higher proportion of its leaf area near the top of the canopy than ryegrass does, so it is likely to lose a greater

proportion of its leaf area than grass when the sward is harvested. But then, Davies and Evans (1990) found that defoliation in spring increased the weight of clover leaf and petiole produced, and the percentage of clover in the sward was increased. Then again, in contrast to this are the findings of Harwig et al. (1987) who reported that some physiological stresses were incurred by clover following defoliation. They found that defoliation induced a rapid and severe decrease (of 80% - 95%) in nitrogenase activity of white clover, which resulted in a drastic reduction in the potential input of symbiotically fixed nitrogen. The authors found that the rapid decline of nitrogenase activity following defoliation was associated with a dramatic decrease in oxygen partial pressure at the site of N fixation, which they concluded was the major factor limiting nitrogenase activity after defoliation.

1.2. *Mathematical modelling*

1.2.1. Definition and advantages of modelling

A model is an abstract (or physical), simplified representation of a system (Thornley, 1976). The model should resemble the system, and if the system is a dynamic one, the model should be capable of simulating its dynamics. Starfield and Bleloch (1986) suggested five reasons for constructing models : (1) to define problems, (2) to organize thoughts, (3) to understand data, (4) to communicate and test understanding, and (5) to make predictions.

When designing a model one is faced with a trade-off between keeping the model simple and yet trying to simulate a complex system as accurately as possible. The more precise the model is made, the more it incorporates the details of the specific system, the greater the possibility that accurate prediciton is possible. However, as the model concentrates more on one aspect of the system, there is an inevitable loss of generality (Starfield & Bleloch, 1986; Keddy, 1989). A modeller should therefore clearly define the objectives at the onset, thereby specifying the output of the model, which will subsequently clarify the model inputs. The model is thus kept as simple as possible without incorporating more detail than necessary.

There are many types of models, eg., word models, physical models and abstract models. Examples of physical models are graphs, maps, and experimental set-ups,; while abstract models are in the form of mathematical equations.

A mathematical model consists of an equation or a set of equations, which represent quantitatively the assumptions or hypotheses that have been made about the real system (Thornley, 1976). Jeffers (1988) described mathematical models as providing a symbolic logic which is capable of describing ideas, and particularly relationships of very great complexity, while at the same time retaining a simplicity and parsimony of statement. These equations, when solved, should enable the modeller to make predictions about the system, without having to do any experimental work on the system. Modelled systems can thus be stressed, disturbed and destroyed quickly, cheaply and ethically. For example, grazing trials conventionally require large tracts of land, many animals and technical expertise over years or decades. However, once the grazing system is simulated, many experiments can be executed on the computer thereby aiding in the identification of the really critical tests for field experimentation (Mentis, 1988).

There are two different approaches to the use of mathematical models in research: mechanistic (or deductive), and empirical (or inductive) models (Thornley, 1976). Empirical models are built around a pre-existing set of data, and simply redescribe the data without providing any real understanding of how the system works (Thornley, 1976; Hunt, 1982). A mechanistic approach, however, has the advantage that the parameters of the model are more likely to be physiologically related, and it might be easier to perceive how crop management or plant breeding techniques could be applied to give higher efficiency (Johnson et al., 1983). A mechanistic model consists of various sub-models, each of which describes a specific function; e.g. photosynthesis, leaf expansion, senescence. Mechanistic models of plant growth can provide a means of understanding individual plant processes to increase our understanding of the integrated system as a whole, and also ultimately provide a reliable predictive tool (Johnson & Thornley, 1983).

When describing an ecological system it is often more appropriate to use a dynamic mechanistic model (Jeffers, 1988).

Jeffers (1988) outlined 3 principle steps involved in dynamic modelling:

(1) It is necessary to identify the dynamic behaviour of the system, and to formulate hypotheses about the interactions that create the behaviour;

(2) A computer simulation model must be created in such a way that it replicates the essential

elements of the behaviour and interactions identified as essential to the system; and

(3) When the behaviour of the model is sufficiently close to the behaviour of the system, the model can be used to understand and explain the cause of observed changes in the real system, and to suggest experiments to be carried out in the evaluation of potential courses of action.

For the purposes of this particular study a dynamic mechanistic model was developed to describe the growth interactions occurring in mixed stands of white clover and perennial ryegrass, with the intention of gaining a better understanding of the interactions between these two crops.

1.2.2. Models describing plant physiological processes

Extensive work has been done towards the development of models describing the various physiological processes which influence plant growth (Charles-Edwards & Thornley, 1973; Johnson & Thornley, 1983; Johnson et al., 1983; Johnson & Thornley, 1984; Charles-Edwards et al., 1986). Most of these models tend to concentrate exclusively on defining the specific processes involved in the growth of an individual plant, without considering how these processes might be altered by the competitive interactions of these plants with other plants of the same, or of another, species. Most of the crop growth models that have been developed, to date, describe the growth dynamics of monoculture crops, with very little work having been done on modelling mixed crop growth.

Plant growth is the result of a number of physiological processes, including photosynthesis, respiration, leaf expansion, translocation and allocation of carbon, nutrient uptake, and senescence. It is difficult to gain an understanding of the underlying processes governing whole plant growth, particularly since these processes are affected by environmental fluctuations over the course of plant development. Mechanistic simulation models of plant growth provide a means of synthesizing existing knowledge of individual plant and crop processes into an integrated framework which may ultimately be useful as a predictive tool (Johnson & Thornley, 1983). Although these models are useful, most of them deal specifically with only one or two of these physiological processes (Johnson & Thornley, 1984; 1985), and

rarely have attempts been made to integrate all these models into one model which describes plant or crop growth as a whole. Below a brief review of some plant physiological models in the literature is presented.

(i) Photosynthetic models

Photosynthesis can be considered at three different levels, the level of the single chloroplast (Farquhar et al., 1980), the single leaf, and the plant or crop level. The photosynthetic models that are most commonly employed by plant ecophysiologists are those concerned with photosynthesis at the single leaf, and plant or crop levels.

There are several detailed models describing the response of single leaf photosynthesis (Rabinowitch, 1951; Zhang, 1988). At the canopy level, however, the model must account for the changing levels of irradiance within the canopy. Those models which scale up to canopy photosynthesis from single leaf photosynthetic models are not accurate representations of the real system since they are based on the assumption that the irradiance is equally distributed to all leaves within the canopy. An accurate representation of canopy photosynthesis would involve an integration of the photosynthesis at the various irradiance levels within the canopy. This would result in a model which would be too complex. Subsequently, most models of canopy photosynthesis that have been developed are either empirical, or semi-empirical models (Thornley, 1976; Johnson & Thornley, 1985). The rectangular hyperbola was the most widely used empirical curve describing single leaf photosynthesis in response to irradiance, but it has become generally accepted that this curve gives a poor fit to experimental data (Marshall & Biscoe, 1980; Monteith, 1981; Zhang, 1988). Marshall & Biscoe (1980) recognised the need for a versatile, semi-empirical model describing the dependence of single leaf photosynthetic rate on irradiance, and whose parameters would be related to physical and chemical processes. Such a model would contain sufficient parameters to account for the major characteristics of photosynthesis-light responses but not so many as to become obscure and cumbersome as an analytical tool. The non-rectangular hyperbola of Rabinowitch (1951) was found to meet these demands. This model accurately described the responses of photosynthesis to irradiance in terms of four useful and biologically meaningful parameters: Amax, the maximum rate of net photosynthesis; α, photochemical efficiency; R_d, rate of dark respiration; and Θ, depending on the ratio of resistances and defining the degree of curvature between the light-limited and

carbon dioxide-limited parts of the response. The non-rectangular hyperbola was found to be a major improvement on the rectangular hyperbola and it gave an extremely good fit to experimental data for leaves of C_3 plants (Marshall and Biscoe, 1980), as well as for wheat and bamboo (Zhang, 1988).

Although the advantages of the Rabinowitch (1951) model are many, there are also several problems encountered with the use of this model for entire canopy systems. The model is based on the assumption that the system is homogeneous, and that each photosynthesizing centre experiences the same local light flux density and CO_2 density (Thornley, 1976). This is not true when considering crop canopy photosynthesis, since the leaves receive different amounts of irradiance depending on their positions within the canopy. The Rabinowitch model cannot, therefore be used as it stands, to describe canopy photosynthesis.

In order to model crop photosynthesis, an assumption must be made concerning the light flux density incident on leaves, and how this varies through the canopy. The Monsi and Saeki (1953) equation for light attenuation through the canopy is commonly used, since it accurately describes the canopy structure characteristics and how these affect the amount of light penetrating a canopy.

Johnson and Thornley (1984) developed an analytical model of instantaneous photosynthesis for a horizontally homogeneous crop canopy with random leaf orientation. The model was based on the use of a non-rectangular hyperbola for leaf photosynthesis response to irradiance, and the Monsi-Saeki theory for the light intercepting characteristics of the canopy. The model also provided an approximate method for calculating daily canopy photosynthesis in fluctuating light and temperature conditions, with an accuracy estimated at 1,5% or better.

This model of Johnson and Thornley (1984) was found to be suitable for use in crop growth models, since it summates the contributions of different leaves in the canopy by integration, to obtain the total canopy photosynthesis. Expressions are also derived which enable the calculated canopy photosynthesis to be easily corrected to allow for the effects of diurnal light and temperature variations. For the above reasons the Johnson and Thornley model (1984) was found to be the most suitable for incorporation into the model developed for the present study of ryegrass and clover, and was used as a sub-model defining canopy photosynthesis (see chapter 2).

(ii) Plant canopy structure and light interception models

An important part of many models of plant and crop growth is concerned with the interaction of the system with the light climate (Thornley, 1976). The way in which this occurs is largely influenced by the plant canopy structure characteristics, such as leaf size, leaf shape, inclination and orientation of leaves. Canopy structure can therefore be important in affecting processes such as photosynthesis, transpiration, leaf expansion, and competition between species in a plant community (Campbell & Norman, 1989). A complete and accurate description of a canopy would be required for modelling light interception and the resultant effects on photosynthesis and plant growth.

The canopies of single, spaced (or isolated) plants are the most difficult to describe mathematically, since the incoming radiant energy must be numerically integrated from all directions in order to estimate the downward light flux density at any point (Charles-Edwards & Thornley, 1973). Such a model would thus need to be treated using two or three coordinates. As a result of this difficulty, less attention has been paid to the isolated plant, even though during the early stages of growth most crops are essentially open arrays of isolated plants, intercepting light more or less independently of one another (Campbell & Norman, 1989).

Crop canopies, however, are less complicated to analyse mathematically than single isolated plants because the downward radiant flux density incident upon a horizontal plane changes in one dimension only, thus reducing the crop problem to one involving a single coordinate (Thornley, 1976). The simplest situation to describe mathematically is when canopy closure occurs (Charles-Edwards et al., 1986). When the plants grow to the point of overlapping (resulting in canopy closure) it becomes difficult to discern the outline of a particular plant or row of plants, and radiative transfer can be treated using the simplified one dimensional model approach.

Charles-Edwards and Thornley (1973) made one of the few attempts to model the light interception of isolated plants. They developed a semi-empirical model for calculating light flux densities within the canopy of an isolated plant. The model was based on several approximations and simplifications in an attempt to provide a relatively simple model, somewhat analogous to that suggested by Monsi & Saeki (1953) for crops. The validity of the model (Charles-Edwards & Thornley, 1973) was not investigated, and so its accuracy has not

been established, although Thornley (1976) advised against its use since he felt that it was not realistic for many plants.

Light interception and absorption by crops have been considered by many workers (Ford & Diggle, 1981; Johnson & Thornley, 1985). Most authors (Johnson & Thornley, 1984; Rimmington, 1984) have used the Monsi & Saeki (1953) model as the basic equation for describing light attenuation through a plant canopy. The Monsi-Saeki model is based on Beer's law and it provides a very convenient equation for empirical application to certain crop canopies (Thornley, 1976).

The Monsi-Saeki (1953) model assumes that the vertically projected irradiance density incident on a canopy has a maximum value, I_o, before entering the crop canopy, and that this light becomes progressively attenuated as it is intercepted by the vertical layers of leaves of the crop canopy. The amount of light intercepted by the leaves in the upper surface of the canopy is determined by the canopy extinction coefficient.

The canopy extinction coefficient is a constant and has values ranging from zero to 1, depending on the inclination of the leaves of a particular plant. A plant with horizontal leaves will have a canopy extinction coefficient value of 1, indicating that most of the incident irradiance is intercepted by the upper canopy surface. If a plant has vertically inclined leaves, the canopy extinction coefficient will have a value approaching zero, and this means that the irradiance passing through a canopy will be more evenly distributed (Campbell & Norman, 1989).

Another factor influencing the distribution of light through a canopy is the planting density. If the planting density is increased then the overall light flux density absorbed will also be increased, but the light flux available per plant will be decreased (Charles-Edwards & Thorpe, 1976).

An example of a model for light attenuation in a crop canopy that was not based on the classic Monsi-Saeki model is the model of Ford and Diggle (1981). These authors modelled the competition for light in a plant monoculture as a spatial stochastic process in relation to differences in plant height. The model was based on the assumption that competition for light is a one-sided process because tall plants suppress short plants but not vice versa. Subsequently, the model has only one measured plant variable, plant height, and competition is formulated as a spatial interaction and is stochastic (i.e. the size of a plants' neighbours are

chance events).

For the purposes of this study we have chosen to model light interception along the basis of the Monsi-Saeki model, as have most other authors (Johnson & Thornley, 1984; 1985; Rimmington, 1984).

(iii) Modelling growth and maintenance respiration

McCree (1970; 1982) recognised two distinct components of the plants' respiratory activity. One, called maintenance respiration, refers to the CO_2 that results from protein breakdown, plus the CO_2 produced in respiratory processes that provide energy for the maintenance processes (Penning de Vries, 1975). Maintenance processes include the processes which maintain cellular structures and gradients of ions and metabolites, and also the processes of physiological adaptations that maintain cells as active units in a changing environment.
The other component, characterised by the growth respiration coefficient, is related to the synthesis of new structural material and metabolic machinery of the plant, and is usually called growth respiration. Growth respiration is equivalent to the carbon lost in the conversion of storage carbon to structural carbon. Growth respiration is thus dependent on the yield efficiency coefficient (Johnson & Thornley, 1985). So, if the yield efficiency of ryegrass is 0.75 (Johnson & Thorley, 1983) then 1 g storage carbon would be converted to 0.75 g structural carbon and 0.25 g carbon would be lost to growth respiration.

The concept of cost is fundamental to understanding how plants function in their environment (Williams et al., 1987), since the manner in which a plant allocates resource expenditure among different organs and different metabolic functions affects its overall growth and performance in a particular environment. Penning de Vries et al. (1974) reported a method for determining the C costs of constructing biological materials that was based on analysis of the metabolic pathways used for producing the organic components of a sample. Although their method is elegant in principle, the multiple biochemical analyses make it laborious, particularly for processing large numbers of samples. Simpler approaches were developed by McDermitt and Loomis (1981) who estimated growth yields from the elemental composition of a sample, and Williams et al. (1987) who estimated growth yields from tissue costs of a

sample.

There are two competing views of the growth and maintenance aspects of plant respiration: a traditional view based on growth analysis which relates respiration to the whole plant dry weight, and a differential equation formulation which distinguishes between storage, degradable and non-degradable components of plant tissue (Thornley, 1977).

Thornley (1977) proposed a model in which plant dry matter was divided into 3 categories: storage material which may be used for growth; non-degradable structural material which cannot be recycled, and which is considered inert; and degradable structural material which is assigned a rate constant of degradation, and which is considered to be biologically active. The model has 4 parameters: 2 yield constants and 2 rate constants. The model has been successfully utilized for steady-state exponential growth in continuous light, respiration in the dark, and $^{14}CO_2$ evolution after a pulse label. Thornley (1977) proposed that his model was a more realistic framework for the consideration of plant growth and respiration than the traditional approach for the following reasons:

i) it avoids treating maintenance as giving rise to a fixed demand for substrate;

ii) it suggests a reason for the very variable estimates of the maintenance requirements that have been made; and

iii) it provides a mechanism for incorporating senescence into plant growth models.

Barnes and Hole (1978) and Loehle (1982) suggested an improvement of both the traditional model of respiration and Thornley's (1977) model would be to reconcile the two models into one model. The growth respiration portion of the traditional model was modified (Loehle, 1982), since this portion of respiration is due to the growth of new cells, so structural biomass replaced total plant weight. The Loehle (1982) model is thus only valid for plants with non-declining components, because of the assumption that losses of degradable components must be replaced.

Thornley (1982) presented a simplified, updated version of the Thornley (1977) model, which defined respiration in a single equation. This model was found to be suitable for application at the plant or organ level, and it may therefore be incorporated into crop growth models.

Penning de Vries (1975) gives various methods of estimating the maintenance costs in plant

cells, and suggests that a better understanding of the maintenance processes may give a clue how to manipulate plant characteristics or the environment to reduce the amount of assimilates consumed in these processes.

(iv) Plant component growth and senescence models

Plant growth has been examined at various levels of complexity: the level of the cell (Dale, 1970), the shoot and root level (Johnson & Thornley, 1987), the leaf level (Johnson & Thornley, 1983; Thornley, 1991), and the whole-plant level (Hunt & Courtney, 1984). Leaf growth, expansion and senescence are amongst the most important processes in plant and crop dynamics, since they make a critical contribution to crop productivity (Thornley, 1991). Leaf responses to environment are complex and there have been few mechanistic models of leaf growth. Crop modellers, however, have a need for a simple mechanistic leaf tissue growth model which can account for the general effects of the environment on leaf characteristics, and which may indicate how leaf responses might be modelled effectively within a crop model. Such a model was developed by Thornley (1991). This was a simple mechanistic model of leaf tissue growth in which the only environmental factors addressed were irradiance and temperature. The model made predictions of final leaf area, the time at which the leaf becomes an exporter, and the time of senescence.

The partitioning of growth between the shoots and roots of plants during vegetative growth has been considered to be an important factor in understanding the growth and yield of plants and crops in response to both shoot and root environments. Several models (Mäkelä, 1986; Johnson & Thornley, 1987) have been developed for the partitioning of newly synthesized dry matter between shoots and roots in vegetative plants. The models of both Mäkelä (1986) and Johnson and Thornley (1987) have dealt with plant growth as being a function only of carbon assimilation by the leaves, and nitrogen uptake by the roots.

Stützel et al. (1988) developed a model for the partitioning of new above-ground dry matter, since they felt that it was inaccurate to consider only the leaf and stem components of the shoot (eg. Johnson & Thornley, 1987). The model of Stützel et al. (1988) distinguishes two types of stem tissue, one directly related to the production of new physiologically active leaf tissues, and the other with the production of tissues necessary for the maintenance of

mechanically stable stem structures. This model provides a means of quantifying the energy costs for stem production of different plant types growing under different conditions.

Models of whole-plant growth have been investigated using a variety of approaches, from traditional growth analysis (Hunt, 1982), through various developments of growth analysis including light conversion analysis, to complex mechanistic models of growth (Warren-Wilson et al., 1986). Jolliffe and Courtney (1984) investigated whole-plant growth using three different techniques: plant growth analysis, yield component analysis, and demographic analysis. Each technique subdivided growth into morphological or physiological components, and several relationships were derived to define the contributions made by the various components to the performance of the whole plant.

Equations describing senescence are found in several models of plant growth (Johnson et al., 1983; Johnson & Thornley, 1985; Thornley, 1991). Senescence is an important aspect of plant growth models, particularly in grasses where the process of senescence enables pastures to be highly adaptable and to withstand grazing. In the model of leaf tissue growth (Thornley, 1991), the onset of senescence was defined as the time at which 'machinery' carbon begins to decline. Johnson and Thornley (1983) modelled senescence on the assumption that there is a loss from the structural material at a constant rate of senescence.

1.2.3. Models of crop monocultures versus models of mixed crop stands

There are many more models of crop growth for monocultures (Johnson & Thornley, 1983; 1984; 1985) in the literature than there are models for mixed crop stands (Rimmington, 1984). Most of the monoculture models in the literature are for grasses, probably because grasses are easily subdivided into four compartments: growing leaves, first and second fully expanded leaves, and senescing leaves (Johnson & Thornley 1983).

The reason for the relatively limited amount of work on models for mixed crop stands is that it is difficult to describe interspecific interactions mathematically in a simple manner. Rimmington (1984) was one of the few authors to analyse the competition for light in mixed plant canopies of ryegrass and clover, and its effect on dry- matter production. The model developed by Rimmington (1984) described the absorption of light by the component species

by accounting for their different optical properties. Rimmington's (1984) model does not however account for the environmentally variable effects of temperature and irradiance on photosynthetic rates. The temperature and irradiance dependence of photosynthesis in monoculture crops was modelled by Johnson & Thornley (1984; 1985).

The main objective of this study was to develop a model which reconciles the growth models of Johnson and Thornley and the Rimmington (1984) model, in an attempt to build a complete, comprehensive model of crop growth for mixed stands of ryegrass and clover.

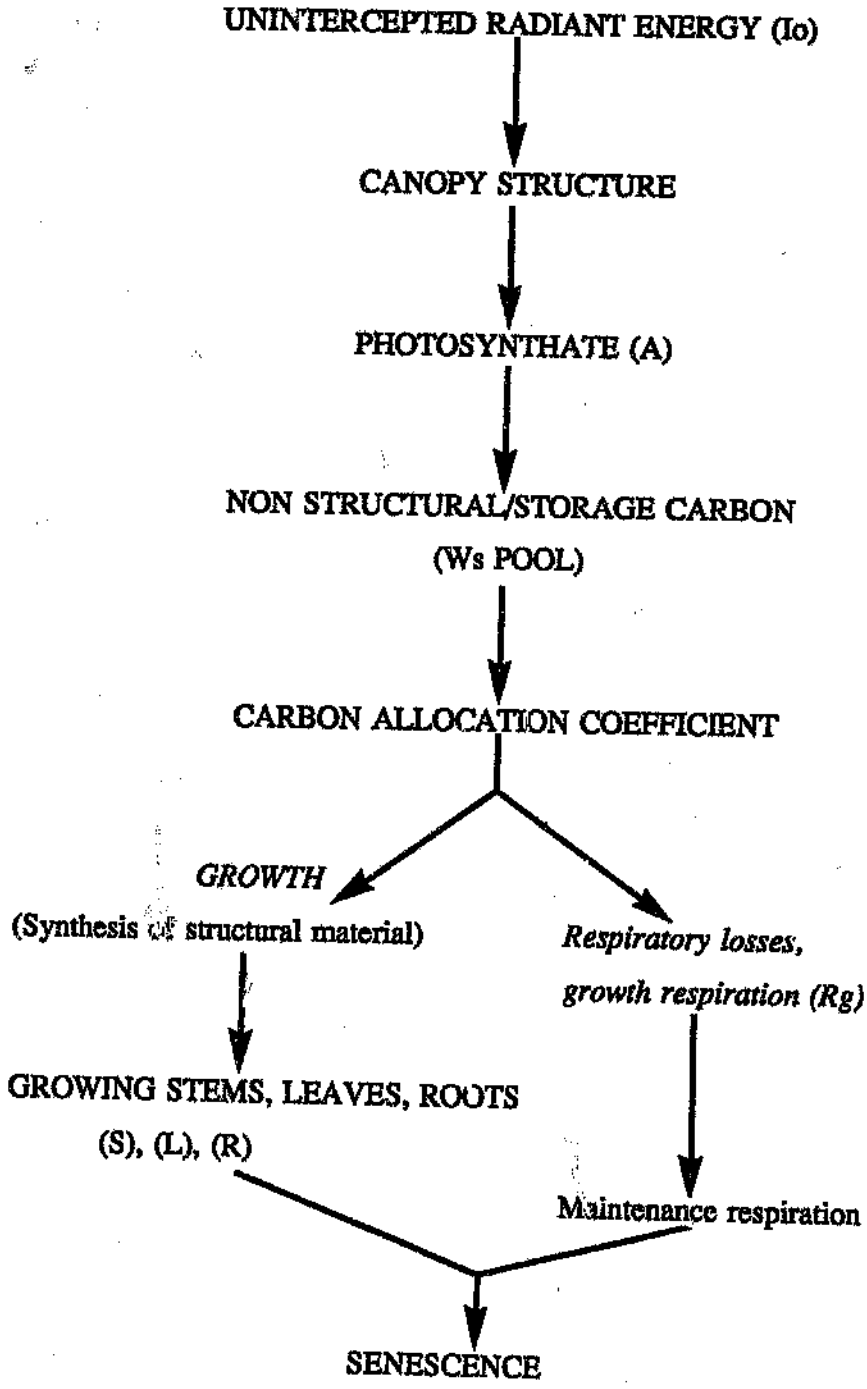


Figure 2.1. Conceptual scheme of the model

CHAPTER 2

CONCEPTUAL DEVELOPMENT OF THE MODEL

2.1. Rationale of the model

The model is based on the assumption that the interspecific competitive ability of 2 species in a mixed stand will depend on their relative efficiencies with regard to the interception of radiant energy. This is determined by the canopy structure/architecture of the respective crops within the mixture, since the canopy structure (leaf orientation and inclination, canopy height, number and position of leaves) determines the amount of irradiance intercepted by each species within a mixed canopy. The amount of intercepted irradiance will determine the relative canopy photosynthetic rates of the 2 species, which will in turn determine their relative growth rates. Only a certain proportion of the fixed carbon will be allocated to respiratory losses and the remainder will be used by the plant for the synthesis of new structural plant material. The proportion of carbon which will be used for the growth of roots, stems, and leaves is determined by the root, stem, and leaf carbon allocation coefficients of the respective crops.

A conceptual scheme for the model is shown in **Figure 2.1.**

2.2. Model formulation

The model consists of several sub-models each of which incorporates definite parameters and/or variables. The model also incorporates a number of differential equations defining the growth of various plant components. Certain parameters such as the quantum yield efficiency (α), the photosynthetic rate at light saturation (Amax), maintenance respiration coefficient (M), the yield efficiency (Y), etc., need to be determined at the onset, either experimentally (see chapter 3), or by sub-models, or from the literature. These parameter values may either be fixed or variable (see section 2.3. on assumptions of the model).

The 'Time-Zero' computer modelling package (Kirchner , 1989) was used for the modelling exercise. 'Time-Zero' was found to be a very user friendly system which allows one to choose from a number of different equation options. Differential equations were used, since this model is a dynamic one. The computer sub-routine for solving differential equations by the Runge-Kutta method was selected.

This chapter will contain the mathematical derivations of the various sub-models and differential equations, as well as a description of the parameters and variables comprising each equation.

2.2.1. Light interception and photosynthesis

In defining canopy photosynthesis, Johnson and Thornley (1983; 1984) have combined an expression for single leaf photosynthesis with Beer's Law of light attenuation through the canopy. Canopy photosynthesis was thus derived by integration of this expression over the canopy cumulative leaf area index.

Beer's law (Monsi & Saeki, 1953) is defined as follows:

$$I = I_o \exp(-kLAI) \qquad (2.1)$$

where I_o is the unintercepted radiant energy entering a canopy; I is the light intensity within the canopy at cumulative leaf area index (LAI). I and I_o have units $J/m^2/s$ photosynthetically active radiation (PAR). k is the canopy extinction coefficient, a dimensionless constant between 0 and 1 which is determined by the angle of the leaves to the normal.

The light flux density incident on the surface of a leaf at depth L, is (Saeki, 1963):

$$I_L = \frac{k}{1-\tau} I = \frac{k}{1-\tau} I_o \exp(-k*LAI) \qquad (2.2)$$

where τ is the leaf transmission coefficient.

The single leaf gross photosynthetic rate (A_L) was defined by the non-rectangular hyperbola (Johnson & Thornley, 1984) as:

$$A_L = \frac{1}{2}\Theta\left[\alpha I + Amax - \left((\alpha I + Amax)^2 - 4\Theta\alpha I Amax\right)^{\frac{1}{2}}\right] \qquad (2.3)$$

where A_L has units kg $CO_2/m^2/s$; Amax is the value of A at light saturation; α is the photochemical/quantum yield efficiency (kg CO_2/J) and is calculated from the initial angle of the curve of photosynthesis (A) versus irradiance (I); Θ is a parameter determining the curvature of the A-I curve. When $\Theta = 0$, then single leaf photosynthesis can be described by the rectangular hyperbola (Johnson & Thornley, 1983) as:

$$A_L = \frac{\alpha I_L Amax}{\alpha I_L + Amax} \qquad (2.4)$$

Equations (2.3) and (2.4) are alternative forms of expressing the A versus I relationship.

The canopy gross photosynthetic rate for a monoculture crop (A_c) is obtained by combining equations (2.2) and (2.4), and integrating through the canopy to give:

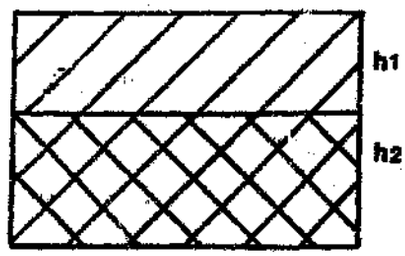
$$A_c = \frac{Amax}{k} \ln\left[\frac{\alpha k I_o + (1-\tau)Amax}{\alpha k I_o \exp(-kL) + (1-\tau)Amax}\right] \qquad (2.5)$$

with units g $C.m^2$ of $ground^{-1}s^{-1}$. (See Appendix D for derivation of equation 2.5).
The daily canopy photosynthetic rate (A_d) is obtained by a further integral:

$$A_d = A_c * day \qquad (2.6)$$

A_d has units kg CO_2 $(m^2$ of ground$)^{-1}$ day^{-1}; day is the daylength in seconds; (a 14 hour day = 50400 s).

Crops within a mixed stand are likely to compete for light, and the species with the better competitive ability is more likely to be the dominant species. The ability to compete for light depends largely on the canopy configuration. The typical type of canopy configuration for a ryegrass and clover mixture is shown in Figure 2.2 (Rimmington, 1984).



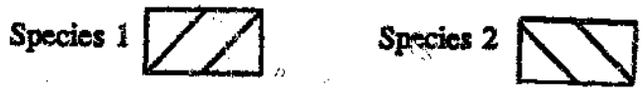


Figure 2.2. Canopy configuration of a mixed ryegrass and clover stand

In this figure it is clearly shown that the ryegrass (species 1) is taller than the clover (species 2) and that consequently the ryegrass can intercept the incoming radiation (I_o) in the upper part of the canopy (h1). Those ryegrass and clover leaves that are in the lower portion of the canopy (h2) will be utilizing a much reduced level of irradiance (I_1) that filtered through from the top of the canopy, and there will be competition between the two species for this light. A mathematical expression for predicting how much irradiance is absorbed by each component within such a canopy was developed by Rimmington (1984):

$$I_1 = (1 - \tau) I_o [(1 - \exp(-k_1 * h_1)] + [1 - \exp(-k_1 * h_1)] * \exp(-k_2 h_2 - k_1 h_1)] / k_1 \qquad (2.7)$$

where I_1 is the irradiance absorbed by species 1 in the upper, unmixed, portion (h1) of the canopy. To determine the amount of irradiance absorbed by species 1 and 2 in the lower, mixed, portion (h2) of the canopy, the following expression was derived (Rimmington, 1984):

$$I_2 = (1 - \tau_2)\ I_0\ [1 - \exp(-k_2 * h_2)] \exp(-k_1 * h_1) / k_2 \qquad (2.8)$$

where I_2 is the irradiance absorbed by species 1 in the lower canopy stratum (h2). This

equation can be similarly used to determine the irradiance absorbed by species 2 (the clover).

We derived an expression for canopy photosynthesis within a mixed sward by combining Rimmington's (1984) expression for light absorption by each component within the canopy (equation 2.8) with the photosynthetic equation (2.5) of Johnson and Thornley (1983). This resulted in the following expression of canopy photosynthesis, which was used in the model:

$$Ac_1 = day*2.303*(Amax_1/k_1)*\log((Amax_1 + \alpha_1*I_o * k_1 * \exp*(-k_2 *LAI_2))/(Amax_1+\alpha_1*I_o * k_1 * \exp(-k_1*LAI_1)*\exp(-k_2*LAI_2))) \quad (2.9)$$

where Ac_1 refers to the canopy photosynthesis of the ryegrass component with units g $C/m^2/day$. The canopy photosynthesis of the clover component (Ac_2) is similarly expressed. Day refers to the daylength in seconds; I - k is the light penetration coefficient (k = 1 - the canopy extinction coefficient); and LAI_1 and LAI_2 are the leaf area indices of ryegrass and clover, respectively.

2.2.2. Growth and partitioning of new structure

The most basic growth model is given by the traditional equation for growth (Thornley, 1977; Jolliffe & Courtney, 1984):

$$\frac{1}{W}\left(\frac{dW}{dt}\right) = R_W \quad (2.10)$$

where W is the total plant dry mass, and R_W is the instantaneous relative growth rate of the whole plant. This is a differential equation and therefore accounts for the changing total plant weight as growth proceeds.

Plant growth and productivity are commonly analysed by procedures which subdivide growth into contributing sub-organismal compartments (Jolliffe & Courtney, 1984) such as leaves, stems, and roots.

Modelling the growth of individual compartments means that the fractional allocation of C into these individual compartments must be considered. The basic growth equation can thus be expanded to give:

$$\frac{1}{W}\left(\frac{dW}{dt}\right) = \left[\frac{1}{L}\left(\frac{dL}{dt}\right)\right]*\left(\frac{L}{W}\right) + \left[\frac{1}{S}\left(\frac{dS}{dt}\right)\right]*\left(\frac{S}{W}\right) + \left[\frac{1}{R}\left(\frac{dR}{dt}\right)\right]*\left(\frac{R}{W}\right) \quad (2.11)$$

where L, S, and R are leaf, stem, and root biomasses, respectively; L/W, S/W, and R/W are the fractional C allocation coefficients into leaves, stems, and roots, respectively.

Since the instantaneous relative plant growth rate $R_W = (1/W)(dW/dt)$, equation (2.10) can be rewritten as:

$$R_W = R_L*\left(\frac{L}{W}\right) + R_S*\left(\frac{S}{W}\right) + R_R*\left(\frac{R}{W}\right) \quad (2.12)$$

The C allocation coefficients, L/W, S/W, and R/W, will be refered to as f_L, f_s, and f_R, respectively. These allocation coefficients should add up to 1. Equation (2.12) can thus be simplified as:

$$\frac{1}{W}\left(\frac{dW}{dt}\right) = R_L*f_L + R_S*f_S + R_R*f_R = R_W \quad (2.13)$$

The accuracy of the C allocation coefficients was tested by solving the above relationship using experimentally derived data.

Table 2.1. Calculated ($\Sigma f*R$) versus experimentally derived (R_W)relative growth rates of mixed ryegrass and clover grown during winter.

Species	f_L*R_L	f_s*R_s	f_R*R_R	$\Sigma f*R$	R_W (exp)
Ryegrass	0.094	0.053	0.087	0.234	0.230
Clover	0.049	0.047	0.015	0.111	0.113

The fact that the empirical data supports this relationship verifies the reliability of all measurements made in the crop growth analysis experiment.

Thornley (1977) expressed the absolute plant growth rate as follows:

$$\frac{dW}{dt} = A - k_{GW_s}(1 - Y) = A - R_p \qquad (2.14)$$

where A is the gross photosynthetic rate; W_s is the storage C dry weight; k_G is the rate at which the storage C is utilized during the growth process; Y is the conversion efficiency of growth, or the efficiency with which storage C is converted into structural carbon; and R_p is the rate of respiration.

In deriving expressions for growth, we combined the equation (2.14) of absolute plant growth rate with the additive relative growth rate differential equation (2.11) of Jolliffe and Courtney (1984). This made it possible to model the growth of the individual plant compartments, both separately and additively.

The absolute growth rates of the leaves (dL/dt), stems(dS/dt), and roots (dR/dt) of the ryegrass are:

$$\frac{dL_1}{dt} = f_{L1} * Y_1 * (A_1 - z * m_1 * W_1) - z * Sn_1 * L_1 \qquad (2.15)$$

$$\frac{dS_1}{dt} = f_{S1} * Y_1 * (A_1 - z * m_1 * W_1) - z * Sn_1 * S_1 \qquad (2.16)$$

$$\frac{dR_1}{dt} = f_{R1} * Y_1 * (A_1 - z * m_1 * W_1) - z * Sn_1 * R_1 \qquad (2.17)$$

where f_{S1}, f_{L1}, and f_{R1} are the fractional carbon allocation coefficients of ryegrass to stems, leaves, and roots, respectively; Y_1 is the yield conversion factor from storage C to structural C, and is approximated as 0.75 for ryegrass (Johnson & Thornley, 1983) and 0.67 for clover (McCree, 1981), A_1 is the ryegrass canopy photosynthetic rate; z is a factor which modifies the rate constants according to temperature and will be defined in detail in the next section; m_1 is the maintenance respiration rate of ryegrass (g C/g C/m^2/day); W_1 is the total plant dry mass (g/m^2); and Sn_1 is the senescence rate of ryegrass.

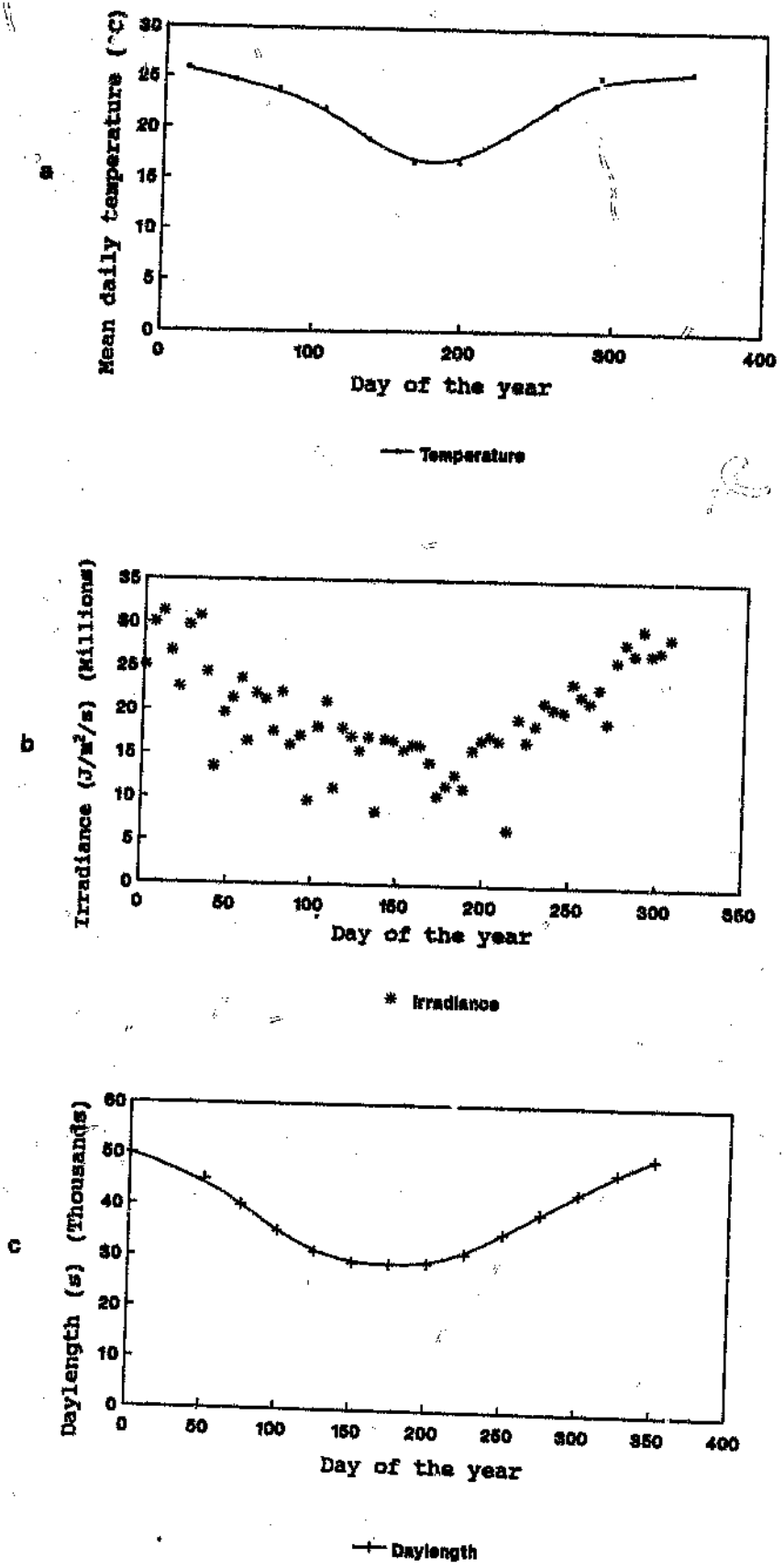


Figure 2.3. Seasonal variations in temperature, irradiance, and daylength over a year.

The absolute growth rate of the entire plant (dW/dt) is the summation of the individual plant components.
The equations above refer to ryegrass, which is species 1 in the model. The clover growth components are similarily defined, and clover is species 2 in the model.

In defining the leaf area index, the same approach was taken as for the above equations. The leaf area index (LAI) can simply be defined as the leaf mass per unit ground (L) * the specific leaf area (δ). The specific leaf area has units m^2 of leaf/g of leaf. In the model the leaf area index is defined as follows:

$$\frac{dLAI_1}{dt} = \delta_1 * f_{L1} * Y_1 * (A_1 - z * m_1 * W_1) - z * Sn_1 * LAI_1 \qquad (2.16)$$

(Note: All the above-mentioned differential equations are repeated in the model with subscripts of 2, and refer to the clover.)

2.2.3. Effects of a variable environment

Some of the above-mentioned parameters are dependent on temperature and irradiance. These include Amax and α, from the photosynthesis equations, and will subsequently also include the growth parameters, since the rate of photosynthesis determines the growth rate of a plant.
In order to describe this temperature dependence it was necessary to model the seasonal variations in temperature and irradiance. The seasonally variable environment was simulated by using equations from Johnson and Thornley (1983), for seasonal variations of daily irradiance (I_o) in J(PAR)/m^2/s, daylength (s/day), and temperature (°C) throughout the year. Several years data were obtained from meteorological records from the University of Witwatersrand Geography library, and a curve fitting procedure was conducted on this data using Enzfitter (Leatherbarrow, 1987) (a non-linear regression analysis program) (fig. 2.3). This resulted in a set of equations defining the environmental variables, which were similar to those of Johnson and Thornley (1983), but which were now applicable to the Southern hemisphere.

These equations are as follows:

$$I_o = 2.49981e^{-7} - 1.0361e^{-7} * (\sin(3.141593*(X1 - 27.854)/365)*\sin(3.141593*(X1 - 27.854)/365)) \quad (2.19)$$

$$day = 4.91853e^{4} - 2.154e^{4} * (\sin(3.141593*(X1 - 1.02135e^{4})/365)*\sin(3.141593*(X1 - 1.02135e^{4})/365)) \quad (2.20)$$

$$T = 20.859 - 9.3111 * (\sin(3.141593*(X1 - 2.46017)/365)*\sin(3.141593*(X1 - 2.46017)/365)) \quad (2.21)$$

where X1 refers to the day of the year, and is defined as:

$$X1 = X + time \quad (2.22)$$

where X is the day of the year when planting was started, and time is the days after planting.

Amax and α were made temperature dependent by fitting the experimental data of Amax and α to a temperature response curve. The curve fitting procedure was done using Enzfitter, and the following definitions for Amax and α were obtained:

$$Amax = Amaxrf*Z \quad (2.23)$$

and,

$$\alpha = alphrf*XZ \quad (2.24)$$

where Amaxrf and alphrf are the optimal temperature values of Amax and α, respectively. z and xz are constants which modifiy photosynthesis and α, respectively, according to temperature, and are defined as:

$$Z = (2*\exp(2.303*2*\log(T + B))*\exp(2.303*2*\log*(T_m + B)) - \exp(2.303*4*\log(T+B))/\exp(2.303*\log(T_m + B)) \quad (2.25)$$

$$XZ = 2*\exp(2.303*2*\log(T+18.13))*\exp(2.303*2*\log(21.97+18.13)) - \exp(2.303*4*\log(T+18.13))/\exp(2.303*4*\log(21.97+18.13)) \quad (2.26)$$

where T is the actual temperature at time X_1, T_m is the temperature at which Amax is maximum; and B is a constant.

The above equations are unique in that they give a temperature adjusted rate of Amax, and a temperature sensitive quantum yield efficiency (α).

2.3. Assumptions of the model

The assumptions of the model are as follows:

1. The canopy extinction coefficient (k) remains constant.
2. Maintenance respiration is assumed to have a similar temperature dependence as photosynthesis and is subsequently also multiplied by the fa[illegible].
3. The yield efficiency (Y) remains constant.
4. Amax and α are the population mean values for a mixed age population of leaves.
5. Amax and α are temperature dependent, and subsequently so is the rate of canopy photosynthesis.
6. The relative plant growth rate = $1/W(dW/dt) = f_L*R_L + f_S*R_S + f_R*R_R$
7. The relative plant growth rate is temperature dependent, and consequently the fractional C allocation coefficients (f) are also temperature dependent.
8. The canopy photosynthetic rate is dependent on the leaf area index (LAI) and the canopy extinction coefficient (k). These two parameters are assumed to be necessary and sufficient for scaling up from individual leaf photosynthesis (based on Amax and α) to canopy photosynthesis via an integration of equation (2.4), with LAI being the variable of integration.
9. The senescence rates of the individual plant compartments are assumed to be equal. Senescence rate is assumed to have a similar temperature dependence as photosynthesis,

hence senescence is multiplied by the factor z.

10. Storage carbon is expressed as (A - z*m*W).

11. Insignificant ontogenetic drift during growth was assumed.

CHAPTER 3

MATERIALS AND METHODS

This chapter includes the materials and methods employed for the derivation of the parameters and state variables needed for the model. These were clearly defined in the previous chapter. In the derivation of the parameters and state variables several experiments were conducted. These included a temperature experiment, an interspecific competition experiment, and an intraspecific competition experiment.

The experimental results and model outputs are presented in chapter 4.

3.1. Temperature experiments

The following experiments were included under this section: (1) the effect of temperature on single leaf photosynthetic rates at varying levels of irradiance; (2) the effect of temperature on biomass and growth rates of ryegrass and clover in monoculture and in mixture; and (3) the effect of temperature on C allocation coefficients of ryegrass and clover.

3.1.1. Photosynthesis-Irradiance measurements at different temperatures

The ryegrass and clover were grown outdoors in pots, for this experiment and were only brought into the laboratory when measurements were being done.

Single leaf photosynthetic rates of ryegrass and clover were measured at different levels of irradiance, and at different temperatures. Photosynthetic measurements were made with a bench-top ADC infra-red gas analyser (IRGA) (model no. 225). A 400 W Siemens mercury vapour lamp was used as the light source, and the levels of irradiance were altered by using various shades of light filters. Irradiance was measured with a Licor photometer (model LI-185 B).

Photosynthetic measurements were made on individual leaves which were clamped into a leaf cuvette. The leaf cuvette was surrounded by a water jacket and was connected to a temperature controlled water bath (Specht, model 55-CB-5). Leaf temperature was monitored by placing a Bailey thermocouple (model BAT-12) in contact with the leaf.

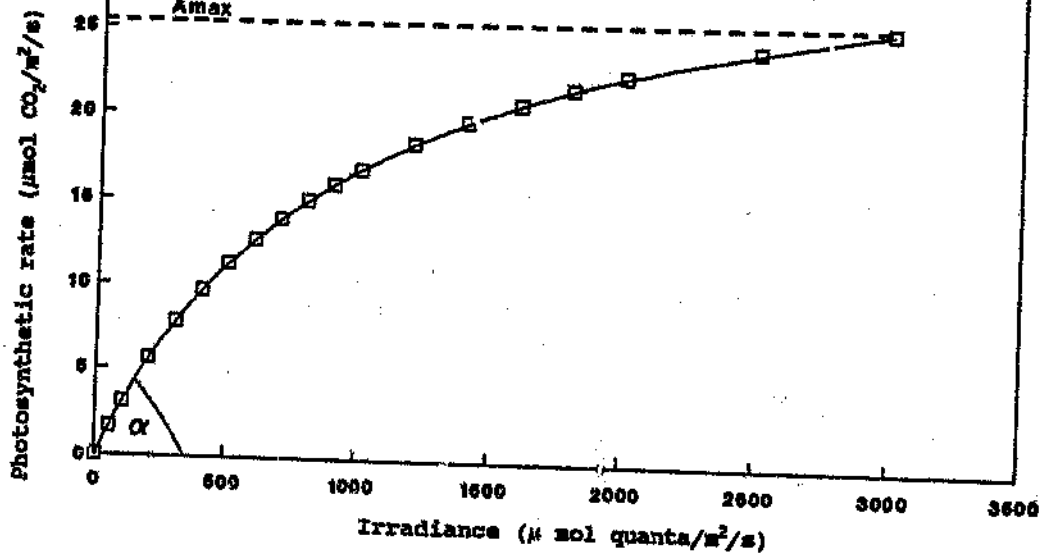


Figure 3.1. Photosynthesis-Irradiance curve for clover at 20°C showing the calculations of Amax and α

Wet and dry bulb temperatures were measured using a whirling hygrometer. The ambient vapour pressure was then calculated and this ranged from 1.8 to 2.6 kPa during photosynthetic measurements.

To calculate the actual rate of leaf photosynthesis (in μmol $CO_2.m^{-2}.s^{-1}$) the following equation was used:

$$A = \frac{\Delta ppm * 10^{-6}}{LA} * \frac{V}{22.416} * \frac{273.15}{T} * \frac{p}{101.3} \qquad (3.1)$$

where A = photosynthetic rate (μmol $CO_2.m^{-2}.s^{-1}$)

V = air flow rate through the cuvette containing the leaf, which was measured as 17.5 cm^3/s.

ppm = the difference in CO_2 of the air streams before and after the assimilation chamber measured at the same temperature and pressure (cm^3m^{-3}). This value must be multiplied by 10^{-6} to convert the ppm to cm^3cm^{-3}.

T = both the temperature at which the flow meter was calibrated and the temperature of the flow meter at the time of observation.

p = barometric pressure at the time of observation (83.5 kPa).

22.416 = ml/mmol of CO_2 at standard temperature and pressure.

LA = leaf area in m^2.

Amax and α values were derived for clover and ryegrass from photosynthesis (A) versus irradiance (I) curves. The A-I curves were generated by a curve fitting procedure using Enzfitter (a non-linear analysis program, which fits the statistically best curve to the data). Amax and α were then calculated from the A-I curves (fig. 3.1) from the following empirical function:

$$A = \frac{Amax * \alpha * I}{Amax + \alpha I} \qquad (3.2)$$

Amax and α were measured at 7 different temperatures for clover : 5°, 10°, 15°, 20°, 25°, 30°,

and 35°C. For the ryegrass it was only possible to obtain Amax and α at 20°, 25°, 30°, and 35°C because at temperatures lower than these the rate of photsynthesis was too low to be detected by the IRGA.
The values of Amax and α that were calculated from this experiment, for ryegrass and clover, were used in the model.

It should be noted here that single leaf photosynthetic rates are easily measured relative to canopy photosynthetic rates. It is extremely difficult to measure canopy photosynthesis accurately since other factors, such as attenuation of light through the canopy and the effects of intra- and interspecific competition, need to be accounted for. Problems associated with scale are encountered when using experimentally derived data for leaf photosynthesis at higher orders of complexity, such as canopy photosynthesis, in the model. The model does, however, try to accomodate such problems by accounting for the light attenuation through the canopy.

Maintenance and growth respiration rates of ryegrass and clover were not measured. Values obtained from the literature were used (Penning de Vries et al., 1974; McCree, 1982).

3.1.2. Biomass and growth rate measurements of ryegrass and clover during autumn and winter

In this experiment ryegrass and clover were grown in stands of monocultures and mixture, during winter and autumn.

a) Preliminary seed study

Ladino variety clover seeds (code 2650) and midmar variety Italian ryegrass seeds (code 2677) were purchased from Distins seed distributors. A preliminary study of seed viability was carried out by growing the seeds in petri dishes, with 10 seeds per dish and 3 replicates each, for ryegrass and clover. It was found that the clover seeds had a germination rate of 60 - 62% compared to the ryegrass seeds which had 97 - 100% germination rate. Consequently, 40% more clover seeds were added in each experiment.

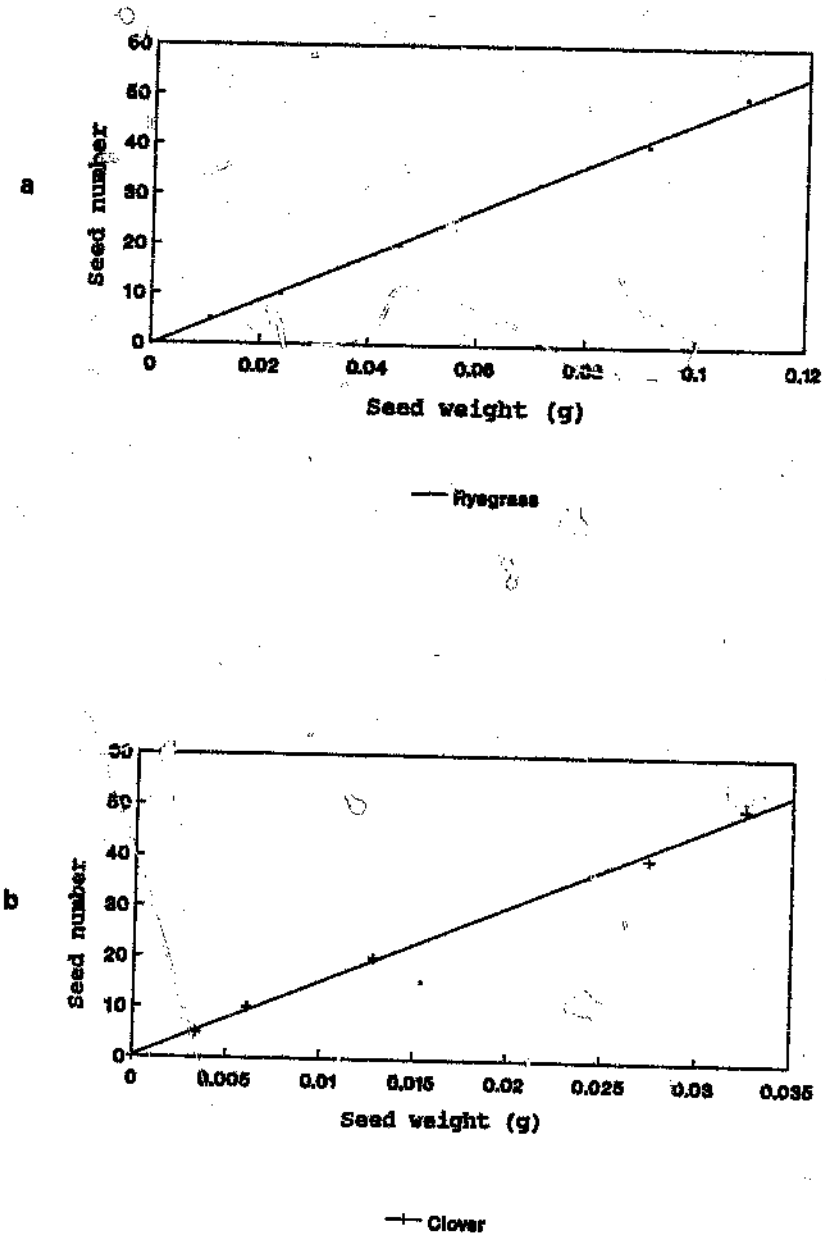


Figure 3.2. Calibration curves for seed number versus seed weight of ryegrass and clover.

To avoid having to count out the seeds for each experiment a calibration curve of seed number versus seed weight was made for both the ryegrass and clover seeds (fig. 3.2). The slope of these curves was calculated and it was thus possible to determine seed number from seed weight, since:

$$seed\ weight = \frac{seed\ number}{slope\ of\ calibration\ curve} \qquad (3.3)$$

b) Above-ground biomass growth rates

Three stands of crops, 3m x 5m in size, were sown in experimental plots on the east campus of the University of the Witwatersrand on the 28/3/90 (winter crop) and again on the 4/2/91 (autumn crop). Each stand was composed of clover only, ryegrass only, and a mixed stand of ryegrass and clover in equal proportions, respectively. The seeds were sown at a high density of 5000 seeds/m^2. An initial 50g/m^2 fertilizer dressing of 2:3:2 N:P:K was applied, and the crops were watered daily to prevent any effects of water stressing. The crops were allowed to grow for approximately 2 months before crop growth measurements were made.

(Note: With ryegrass and clover it is difficult to separate individuals in the field due to tiller formation in ryegrass and internoding along the stolons in clover. Therefore, density will be defined as the initial sowing density.)

Three replicate 100 cm^2 samples were harvested weekly from each stand for 7 weeks. The samples were oven dried at 70°C, weighed and then the mean above-ground dry weights were recorded weekly. The relative daily shoot growth rates of the respective crops were calculated, for winter and autumn, as follows (Hunt, 1982):

$$R_{sh} = \frac{\ln W_2 - W_1}{T_2 - T_1} \qquad (3.4)$$

where W_1 and W_2 are the living above ground dry masses at time 1 (T_1) and time 2 (T_2), respectively.

The dry weights were all multiplied by 10 to convert to g/m^2.

c) Shoot:Root ratios

Stainless steel soil corers of length 20 cm and diameter 4,8 cm (area $1.8 \times 10^{-3} m^2$) were knocked into the ground and were removed with the shoots and roots intact. Three replicate random samples were taken from each stand. The samples were then immediately placed into a cold room at ±5°C to prevent any decomposition occurring. The shoots were then carefully separated from the roots. In order to remove all the soil particles from the roots, without losing too many of the finer roots, the following procedure was carried out:- Each sample was placed into a sieve which was suspended in a bucket of water, so that the water level just covered the sample. The bucket was then placed on a stirrer and was gently shaken. This resulted in the soil particles being dislodged from the roots and dissolving in the water while the roots remained in the sieve. When the roots were clean they were oven dried, together with their accompanying shoots, at 70°C for ± 1 week. (Note: In the case of the mixed ryegrass and clover samples, the shoots were left attached to the roots during the root cleaning procedure. This made it easier to identify which roots belonged to which species, since even though clover roots have nodules, these are not always present along the entire length of each root.)

The dried roots and shoots were weighed and the shoot:root ratios were calculated as follows (Hunt, 1982): shoot dry weight/root dry weight.

Shoot:root ratios were recorded weekly for each stand, over a period of 5 weeks, during both winter and autumn.

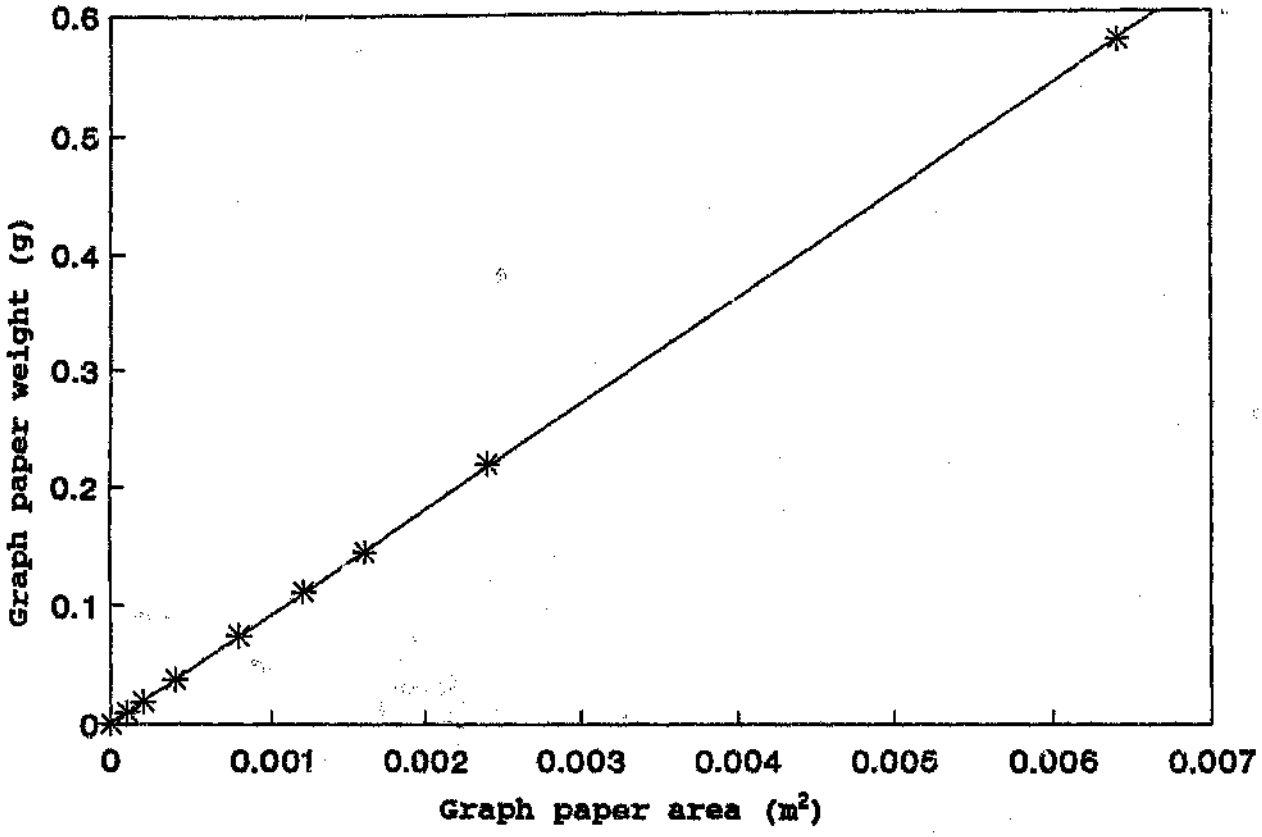


Figure 3.3. Graph paper calibration curve of graph paper weight versus graph paper area.

d) Leaf:Stem ratios

In each stand, three replicate samples were harvested and the leaves were separated from the stems. The samples were oven dried at 70°C and the dry weights of the leaves and stems were recorded. The leaf:stem ratio was calculated as follows (Hunt, 1982):

$$leaf{:}stem\ ratio = \frac{leaf\ dry\ weight}{leaf + stem\ dry\ weights} \qquad (3.5)$$

The leaf:stem ratio was recorded weekly for 7 weeks, for each stand during winter and autumn.

e) Determination of C allocation coefficients

The nett carbon allocation coefficients were calculated from the dry weights of the various plant components as follows:

$$Nett\ leaf\ C\ allocation\ coefficient = \frac{leaf\ dry\ weight}{total\ plant\ dry\ weight} \qquad (3.6)$$

And, similarly for the nett stem and root C allocation coefficients.

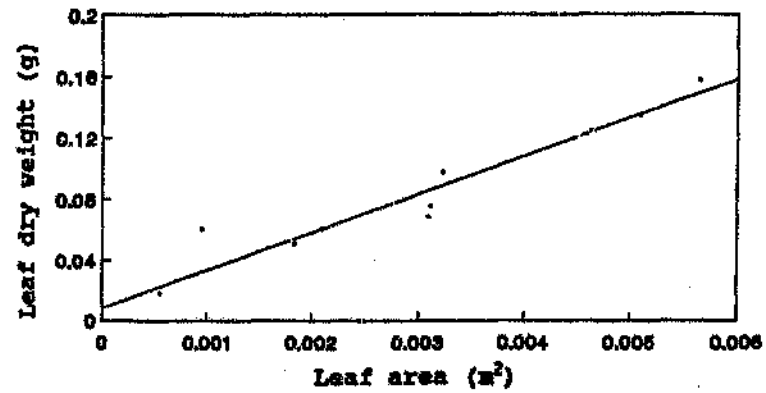
f) Leaf area measurements

A technique for determining leaf area directly from leaf dry weight was perfected. A graph paper calibration curve was made by weighing pieces of graph paper of known area and plotting graph paper weight versus graph paper area (fig. 3.3).

Samples of leaves from each stand were harvested and traced onto graph paper, and the leaf area was determined as follows:

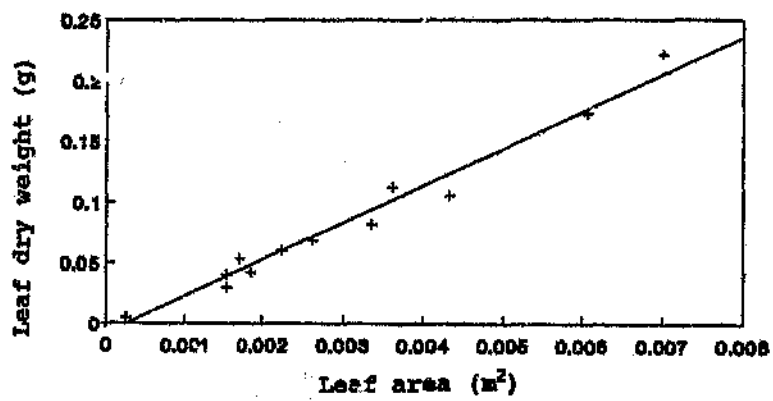
$$leaf\ area = \frac{weight\ of\ graph\ paper}{slope\ of\ calibration\ curve} \qquad (3.7)$$

a



Ryegrass

b



Clover

Figure 3.4. Calibration curves of leaf dry weight versus leaf area for ryegrass and clover.

The dry weight of these leaves was also recorded, and after several measurements it was possible to plot leaf dry weight versus leaf area for both ryegrass and clover (fig. 3.4). The leaf area was then directly determined from the leaf dry weight using the following equation:

$$\text{leaf area} = \frac{\text{leaf dry weight}}{\text{slope of leaf dry weight vs. leaf area curve}} \quad (3.8)$$

The leaf area per gram of dry material for ryegrass and clover, in monoculture and in mixture, was recorded weekly for 7 weeks.

The leaf area per m^2 ,or leaf area index (LAI) was subsequently calculated as follows (Hunt, 1982):

LAI = shoot dry mass(g/m^2) * leaf area per gram * leaf:stem ratio

The LAI of ryegrass and clover, in monoculture and in mixture, was calculated weekly over a 7 week harvest period, during winter and autumn.

g) Canopy height

Approximately 10 replicate measurements of canopy height were taken, for each stand, using a tape measure. Measurements were made from the ground to the highest point reached by the majority of leaves. The mean canopy height for each stand was recorded weekly, for 7 weeks during winter and autumn.

3.2. Interspecific competition experiment

An experiment was devised, as per Rimmington (1984), to determine the effects of interspecific competition on ryegrass and clover.

Five stands of crops were planted on the 26/03/91 at a constant sowing density of 2500 seeds/m^2 per stand. Three of the five stands were mixed with ryegrass and clover in the following proportions:

3 ryegrass : 1 clover

1 ryegrass : 1 clover

1 ryegrass : 3 clover

The remaining 2 stands were the controls, with ryegrass only and clover only, respectively.

3.2.1. Crop growth analysis measurements

The crops were allowed to grow for ± 2 months and the following data (as above) was collected from each stand:

i) Total shoot dry mass

ii) Total root dry mass

iii) Shoot:root ratios

iv) Leaf:stem ratios

v) Determination of C allocation coefficients

vi) Leaf area per leaf mass

vii) LAI

viii) Canopy heights

The data was collected over three harvests which were taken at two week intervals; ie. over a period of 6 weeks in total.

3.2.2. Determination of total N contents in the leaves, stems, and roots of ryegrass and clover

The Dorich and Nelson (1983) method was used to determine total N content in the leaves, stems and roots of ryegrass and clover in the different mixtures (3 ryegrass:1 clover; 1 ryegrass: 1 clover; and 1 ryegrass:3 clover) of the interspecific competition experiment. The ryegrass and clover monocultures were the controls.

Samples of ryegrass and clover leaves, stems, and roots, from the 5 different stands, were separated and dried at 60°C (because N volatilizes above this temperature), and then milled using a 0.5 mm sieve.

The digestion procedure of the ground plant material was as follows:

- 0.1 g of ground plant material was added to a small amount of selenium catalyst mixture and 4.4 ml digestion mixture (Appendix A), in a digestion tube. These were digested at 360°C for 2 hours, or until the solution was clear.
- The solutions were allowed to cool and 50 ml of water was added to each tube. When the solutions cooled down again, they were volumetrically made up to 100 ml and mixed well.
- 12 digested blanks were also prepared for use as the standards.

A stock solution (Appendix A) was prepared, and this was used to make an intermediate stock solution by adding 2 ml of stock solution to 100 ml of distilled water. 0, 1, 2, 3, 4, and 5 mls of intermediate stock were then diluted to 100 ml, and the 4.4 ml of digested blanks were added to these, respectively. (There were 2 replicates of each standard).

The determination of ammonium nitrogen was carried out as follows:

- 1 ml of the digested plant material was transfered to 25 ml volumetric flasks. To this was added 1 ml of solution B (Appendix A) and the solution turned bright pink. Solution A (Appendix A) was added with a dropper until the solution just turned back to yellow. This procedure ensured that the solution was in the right pH range.

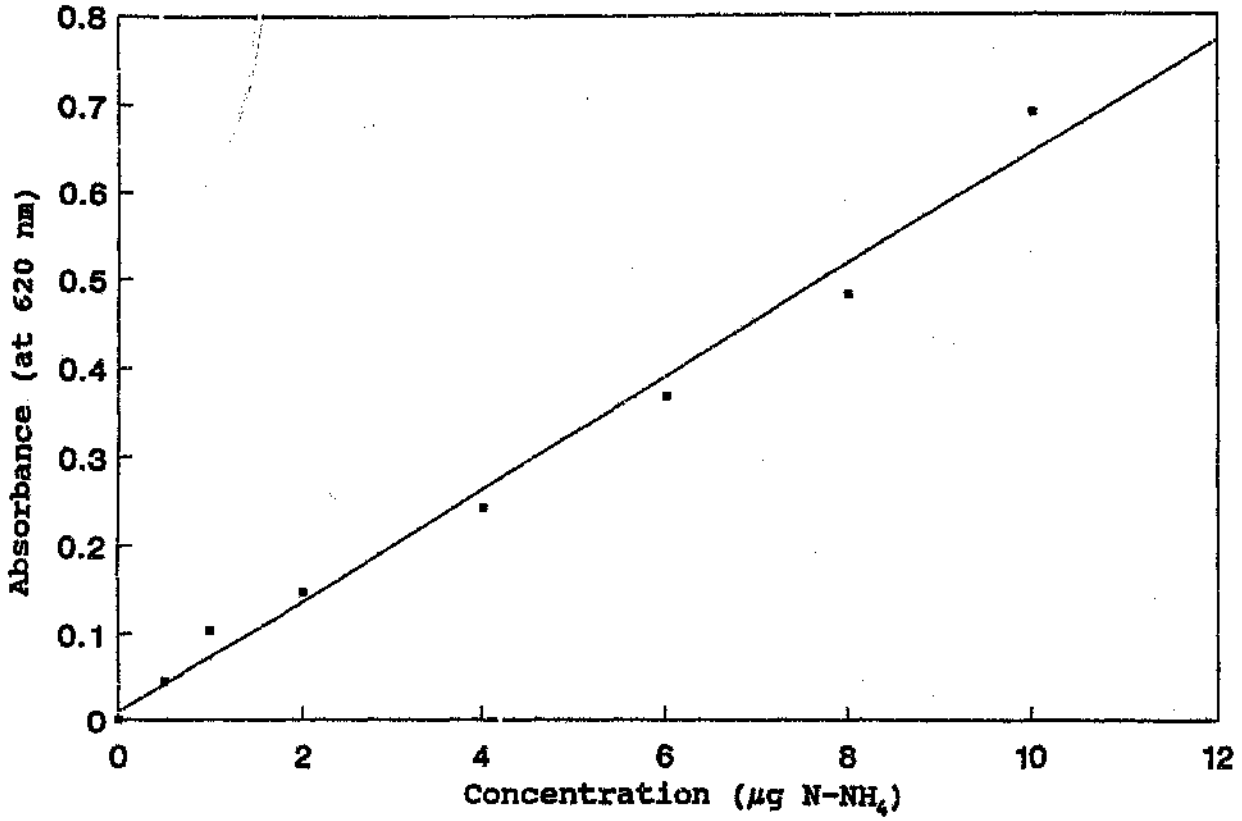


Figure 3.5. Standard curve for the determination of N-NH_4 concentration.

- 2 ml of solution C followed by 4 ml of solution D (Appendix A) were then added, and the flasks were made up to volume with de-ionized water and left at room temperature for an hour. The solutions were then a greeny-blue colour.

- The standards were treated to the exact same procedure, except that 5 ml of digest was tranfered to the 25 ml volumetric flasks, instead of 1 ml. The standards represented 0, 1, 2, 3, 4, and 5 µg $N\text{-}NH_4$, respectively.

- The absorbances of the standards were read at 620 nm on a UV visible spectrophotometer (model DHS 90). A standard curve was then made by plotting absorbance versus concentration (µg $N\text{-}NH_4$) (fig. 3.5).

- Finally, the concentrations of the samples were calculated from the standards, and the actual N concentrations were calculated from:

$$\mu g\ N/g\ plant = conc.\ samples * 100(total\ volume) * \frac{1}{vol.\ used} * \frac{1}{W} \qquad (3.9)$$

where W is the mass of ground plant material used for the digestion.

The advantages of using this method for N determination are that only one digestion is required to bring nearly all of the nutrients into solution, no volatilisation of N occurs, and the method is simple and rapid.

3.3. Intraspecific competition experiment

This experiment was carried out to determine the effects of intraspecific competition/initial sowing density on the growth and C allocation coefficients of ryegrass and clover.

Ryegrass only and clover only were planted in pots of diameter 20 cm (area = 0.03 m^2), on the 21/5/91. The seeds were sown at the following densities: 500, 1000, 2000, 3000, 4000, and 5000 seeds/m^2.

For each density 6 replicates were grown; ie. 36 pots per crop.

Three replicate pots for each density were harvested twice, over a 2 week harvest interval, and the following data were recorded:

i) Canopy height

ii) Total shoot dry mass

iii) Leaf area index

iv) C allocation coefficients

The materials and methods for these are oulined in detail in section 3.1.

Note: All the dry masses were multiplied by 31.83 to convert to g/m^2, since the area of each pot was 0.03 m2.

3.4. Statistics

A multi-variate statistical analysis (MANOVA) was carried out on all the unprocessed data of growth rates, C allocation coefficients, and N concentrations of all the above-mentioned experiments. This was done using the SAS system general linear models procedure.

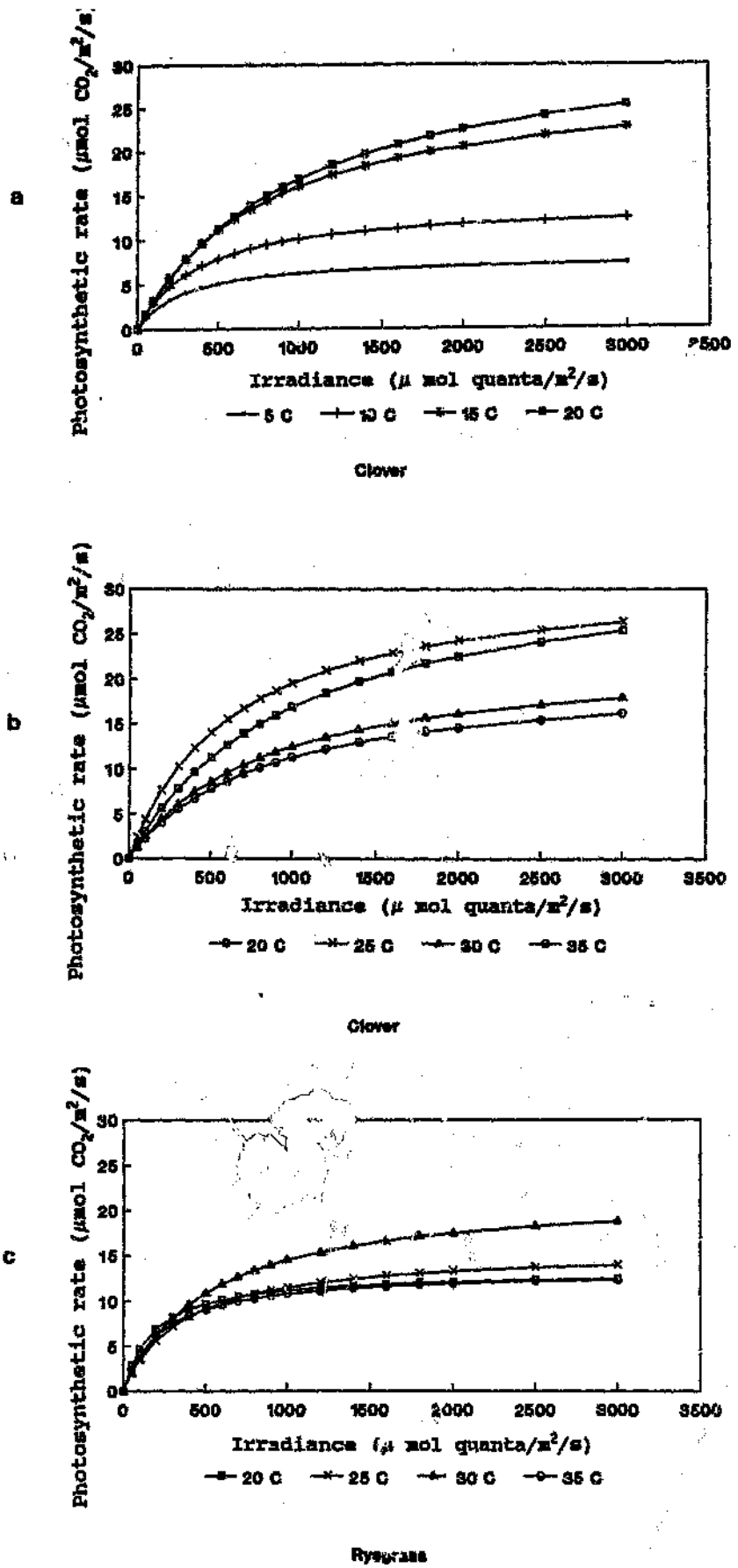


Figure 4.1. Photosynthesis-Irradiance curves for ryegrass and clover.

CHAPTER 4

RESULTS

This chapter has been divided into 2 main sections, the first dealing with the experimental results, and the second consisting of comparisons between model outputs and experimental data. All the means of the experimental data and the model outputs are presented in table form in Appendix C.

4.1. EXPERIMENTAL RESULTS

4.1.1. Temperature experiment

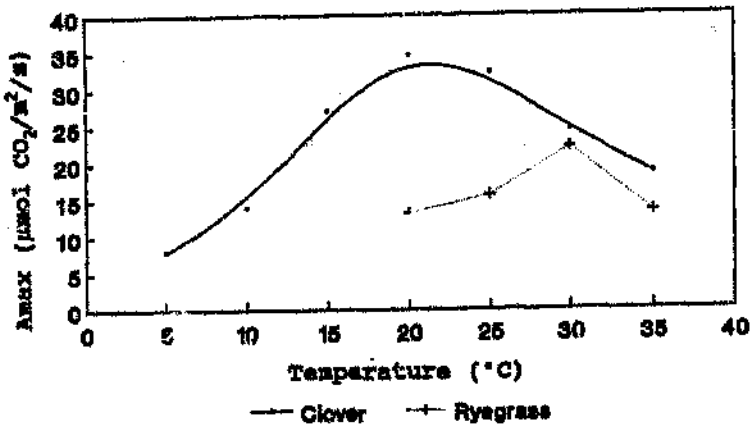
a) Effect of temperature on single leaf photosynthetic rates

The single leaf photosynthetic rates of ryegrass and clover were measured at various levels of irradiance and at different temperatures. Photosynthesis-Irradiance (A-I) response curves for clover were measured at temperatures of 5°, 10°, 15°, 20°, 25°, 30°, and 35°C (**fig. 4.1a**). A-I curves for ryegrass were measured at temperatures of 20°, 25°, 30°, and 35°C (**fig. 4.1b**). The A-I curves for ryegrass and clover were used for the calculations of Amax (the maximum photosynthetic rate at light saturation), and α (the quantum yield efficiency), at the different temperatures measured, by a curve-fitting procedure using Enzfitter.

Amax versus temperature (**fig. 4.2**), and α versus temperature (**fig. 4.3**) curves were then plotted for both ryegrass and clover (the data are presented as a table in Appendix B).
The following results were obtained from this experiment:

- At 20°C, the maximum rate of photosynthesis at light saturation (Amax) of clover was 34,5 µmol $CO_2/m^2/s$ (= 1.52×10^{-6} kg $CO_2/m^2/s$) and Amax of ryegrass was only 14,4 µmol $CO_2/m^2/s$ (= 0.634×10^{-6} kg $CO_2/m^2/s$); i.e. at 20°C clover had a single leaf photosynthetic rate that was ± 2,5 times higher than that of the ryegrass.

a



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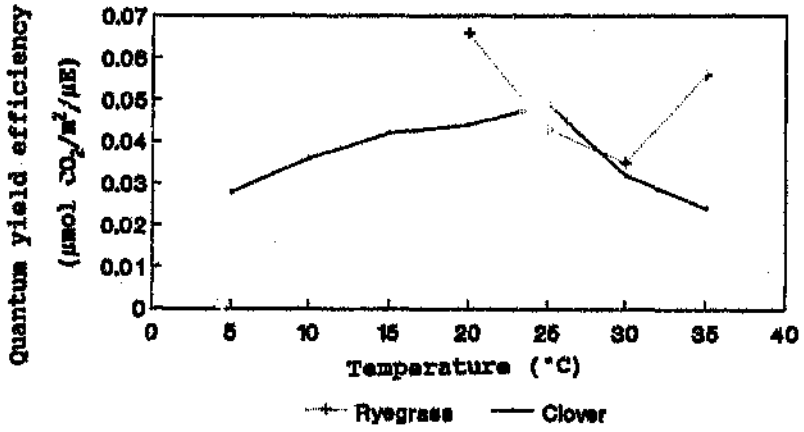


Figures 4.2 and 4.3. Amax and α responses to temperature for ryegrass and clover.

These values of Amax (20°C) compare very well with those of Johnson and Thornley (1983; 1985), which were in the range of 0.6 x 10^{-6} to 1.5 x 10^{-6} kg CO2/m^2/s for grasses.
At 30°C, ryegrass and clover had very similar rates of photosynthesis of 23,7 µmol $CO_2/m^2/s$ (1.04 x 10^{-6} kg CO2/m^2/s) and 24,3 µmol $CO_2/m^2/s$ (1.07 x 10^{-6} kg $CO_2/m^2/s$), respectively. These results suggest that clover would have a faster growth rate than ryegrass when grown in monoculture during the temperate seasons of the year (spring/autumn), but during the hot summer months the 2 crops would be expected to have similar rates of growth.

The apparent competitive advantages of clover due to higher Amax values than r_ grass at the single leaf level are not, however, an accurate reflection of how these crops would behave within a canopy situation. Other factors such as canopy structure (leaf inclination, leaf distribution), quantum yield efficiency, and consequent ability to intercept incoming radiation, by the respective crops, may override the apparant competitive advantages at the sinlge leaf level. Such problems associated with scale and process need to be considered before any predictions can be made from single leaf photosynthetic data, of the overall behaviour of crops within a canopy.

- At 20°C, the quantum yield efficiency (α) of ryegrass was 0.066 µmol $CO_2/\mu E$ (= 1.24 x 10^{-8} kg CO_2/J) and α of clover was only 0.044 µmol $CO_2/\mu E$ (= 8.24 x 10^{-9} kg CO_2/J) (fig. 4.3); i.e. at 20°C, α of ryegrass was 1.5 times higher than that of clover. These values of α (at 20°C) are very similar to those of Johnson and Thornley (1983; 1985) which ranged between 1.0 x 10^{-8} kg CO_2/J and 12 x 10^{-9} kg CO_2/J for grasses.
At 30°C, ryegrass and clover had very similar quantum yield effiencies of 0.035 µmol $CO_2/\mu E$ (6.55 x 10^{-9} kg CO_2/J) and 0.032 µmol $CO_2/\mu E$ (6 x 10^{-9} kg CO_2/J), respectively.
Although clover had a much higher rate of light saturated photosynthesis (Amax) at 20°C than ryegrass, the ryegrass had a higher quantum yield efficiency than the clover. This suggests that ryegrass makes more efficient use of lower levels of irradiance than does clover. This would be of benefit to ryegrass in a canopy situation where there is attenuation of light through the canopy. Added to this, the ryegrass would be at an even greater advantage than the clover in a canopy, since the vertically inclined leaves of ryegrass would allow more light to filter through a ryegrass canopy than would the horizontally inclined leaves of clover.

To test the performance of ryegrass and clover in a canopy situation, the canopy photosynthetic rates of these two crops (as monocultures) were calculated, using the expression for canopy photosynthesis given by Johnson and Thornley (1984):

$$A_c = \frac{Amax}{k} \ln\left[\frac{Amax + \alpha * I * k}{Amax + \alpha * I * k \exp(-kL)}\right] \qquad (4.1)$$

where, A_c has units (g $CO_2/m^2/h$); k is the canopy extinction coefficient which was 0.25 for ryegrass and 0.7 for clover (Loomis & Williams, 1969); L is the leaf area index (m^2 leaf/m^2 ground). The level of irradiance (I), and the daylength (day) were taken from a randomly selected day of the year of which the temperature was 20°C; I was $2.26*10^7$ J/m^2/day, with 48387 seconds in the day, so the mean daily irradiance = 468 J/m^2/s.

The above equation includes the light saturated rate of photosynthesis (Amax), which was significantly higher for the clover than the ryegrass at 20°C, the quantum yield efficiency (α), and the canopy extinction coefficient (k), which is a function of the canopy structure. The two parameters, α and k, are assumed to be necessary and sufficient for scaling up from individual leaf photosynthesis to canopy photosynthesis via an integration of the above equation, with the leaf area index being the variable of integration.

If the canopy photosynthetic rate of ryegrass is higher than that of the clover, under the same environmental conditions, then it can be assumed that the quantum yield efficiency and the canopy extinction coefficient override the effects of a high single leaf photosynthetic rate.

Table 4.1. Canopy photosynthetic rates (A_c) of ryegrass and clover at different leaf area indices.

Leaf area index (m^2leaf/m^2ground)	A_c (Ryegrass) (g $CO_2/m^2/h$)	A_c (Clover) (g $CO_2/m^2/h$)
0.25	0.392	0.866
0.50	0.777	1.671
1.0	1.523	3.092
2.0	2.914	5.184
4.0	5.279	7.100
6.0	7.689	7.309
8.0	8.380	7.727
10.0	9.270	7.735

The calculated rates of canopy photosynthesis (table 4.1) are comparable with canopy photosynthetic rates in the literature. Woledge and Leafe (1976) measured the canopy photosynthesis of ryegrass as 0.5 g $CO_2/m^2/h$ when the leaf area index was less than 1, as 6.5 g $CO_2/m^2/h$ at a LAI of 3, and as 8.8 g $CO_2/m^2/h$ at a LAI of 6. Woledge et al. (1989) measured the rates of photosynthesis within mixed ryegrass/clover swards as 0.83 g $CO_2/m^2/h$ at a LAI of 1.4, with a maximum photosynthetic rate of 3.5 g $CO_2/m^2/h$ at a LAI of 2.06. These authors found that on all occassions clover fixed a smaller proportion of the total ^{14}C fixed by the canopy than its proportion of leaf area.

Table 4.1. shows that the calculated canopy photosynthetic rates of clover were higher than those of the ryegrass (not 2.5 times higher as was depicted by Amax) when the leaf area index was 4 or less. As the LAI increased to between 6 and 10, the canopy photosynthetic rate of the ryegrass exceeded that of the clover. The lower rates of clover canopy photosynthesis at

the higher LAI's, relative to the ryegrass, is a function of the horizontally inclined leaves of clover, which at high LAI results in the upper leaf layer forming a closed canopy thus preventing light penetration within the canopy. This results in lower levels of irradiance within the clover canopy relative to the ryegrass canopy and, consequently lower clover canopy photosynthetic rates. The poorer ability of the clover, relative to the ryegrass, to utilize lower levels of irradiance (ie. the quantum yield efficiency) further decreases the amount of assimilate produced by the clover at high LAI.

The above data proves that single leaf photosynthetic data cannot be used to predict canopy photosynthetic rates when the quantum yield efficiency and the canopy structure are not considered.

The above data also provides an explanation of the differences in growth rates between [illegible] and clover (next section) with regard to differences in single leaf photosynthetic rates.

[illegible]perature on growth rates of clover and ryegrass in monoculture and in mixture

Total plant growth rates of ryegrass and clover monocultures and mixtures were calculated, over a 6 week harvest interval, for the winter of 1990 and the autumn of 1991. Growth was studied in the winter since this is the time that forage crops are usually grown for forage supply to grazers, in South Africa.

The mean weekly temperatures, and the corresponding growth rates, over the winter and autumn harvest periods are presented in **fig. 4.4.** This figure shows that the weekly growth rates ($week^{-1}$) of both ryegrass and clover were strongly dependent on the environmental temperature changes. **Figure 4.4(a)** shows that the growth rate of the ryegrass decreased, from 0.47 to 0.08 $g.g^{-1}.week^{-1}$ as the temperature dropped from 13.5°C to 8°C during the winter, while **figure 4.4(b)** clearly shows an increase in the growth rate of the ryegrass, from

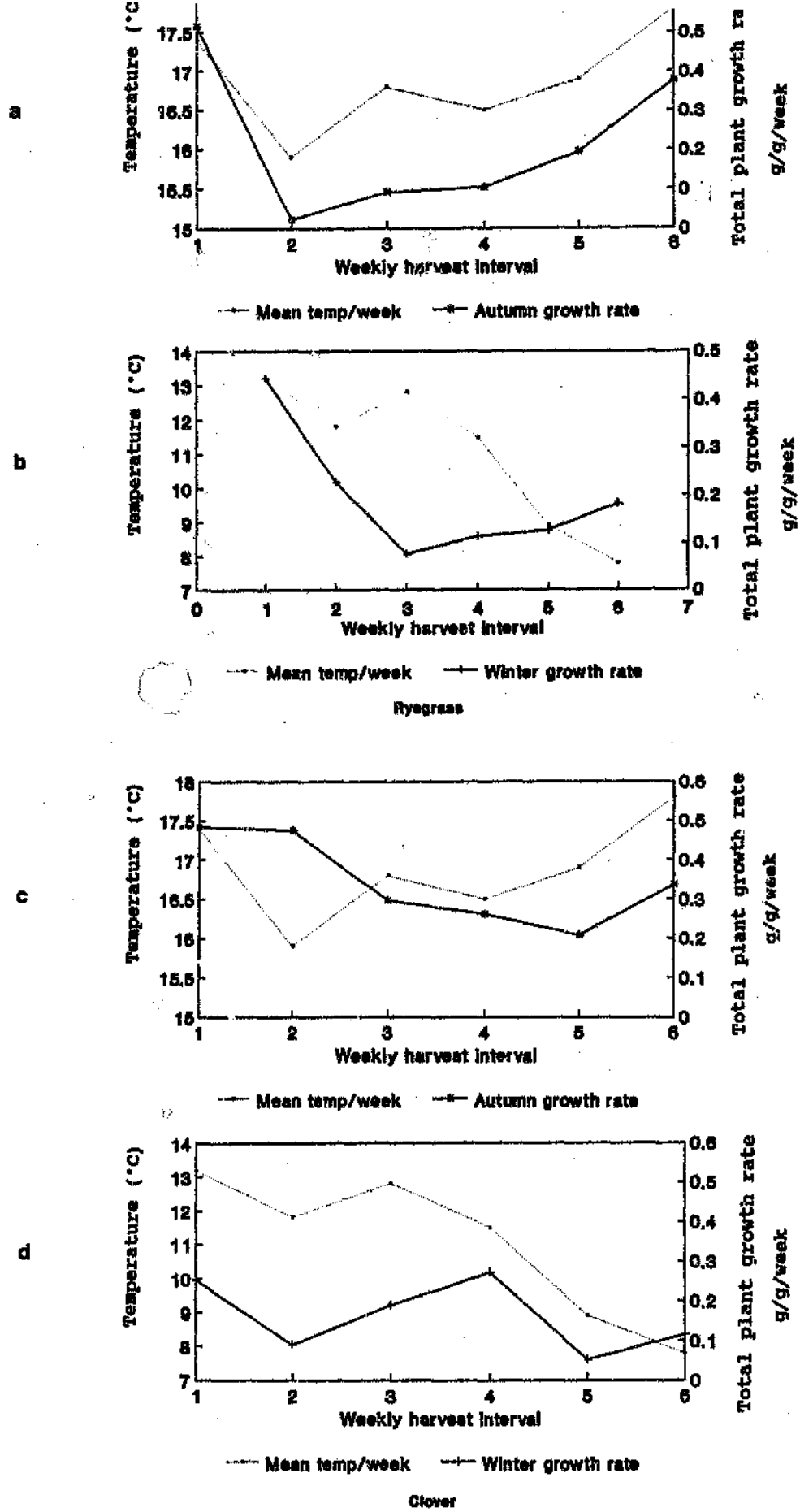


Figure 4.4. Mean weekly temperatures and corresponding growth rates of ryegrass and clover during autumn and winter.

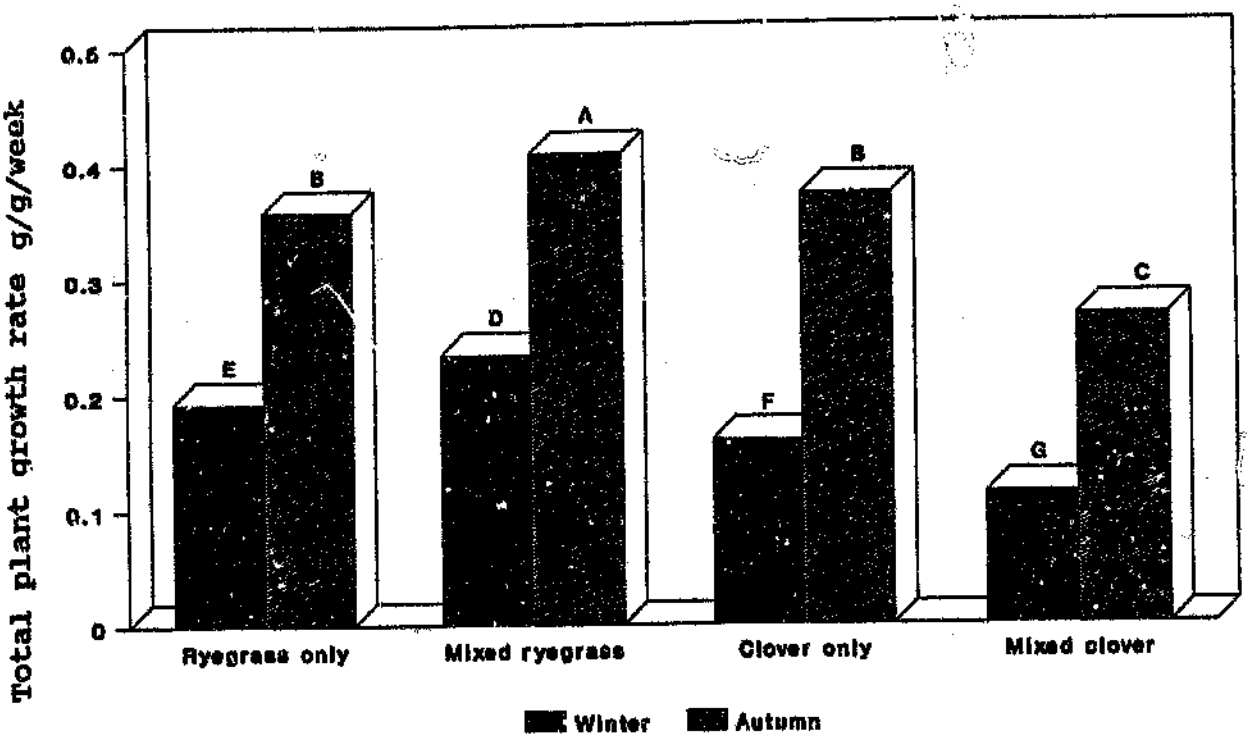
0.01 to 0.395 $g.g^{-1}.week^{-1}$, as the temperature increased from 16°C to ± 18°C. **Figures 4.4(c & d)** show similar trends for clover where the growth rate decreased from 0.26 to 0.11 $g.g^{-1}.week^{-1}$, as the temperature dropped from 13.5°C to 8°C, and increased from 0.3 to 0.35 $g.g^{-1}.week^{-1}$ as the temperature increased from 16° to 18°C.

A comparison of the mean growth rates of ryegrass and clover, as monocultures and as mixtures, was made for winter and autumn.

Figure 4.5 clearly shows that both ryegrass and clover, in both monoculture and in mixture, grew significantly faster during autumn than during winter. In fact, the mean growth rates during autumn were ± double the growth rates during winter, in every case.

There was no significant difference between the growth rates of ryegrass and clover monocultures during autumn (0.36 and 0.37 $g.g^{-1}.week^{-1}$, respectively), but the growth rate of the ryegrass monoculture during winter (0.19 $g.g^{-1}.week^{-1}$) was significantly higher than that of the clover monoculture (0.162 $g.g^{-1}.week^{-1}$). This contradicts the results of the single leaf photosynthetic experiment (fig. 4.2) which showed that the single leaf photosynthetic rates of the ryegrass were generally lower than the single leaf photosynthetic rates of the clover, at the same temperatures. But, as was already discussed, it is inaccurate to predict the performance of a crop canopy from results of single leaf photosynthetic rates, since canopy structure is not accounted for, and ryegrass and clover have different canopy extinction cofficients. This was clearly shown in **Table 4.1.**

Figure 4.5. also shows that the ryegrass grown in mixture with clover (mixed ryegrass) had a significantly faster growth rate than the ryegrass grown in monoculture, both in winter and autumn. The clover, however, had a faster growth rate when grown as a monoculture than when grown in mixture with ryegrass (mixed clover). These results will be discussed in detail under the section dealing with interspecific competition.



Means with the same letter are not significantly different (Pr>F = 0.0001).

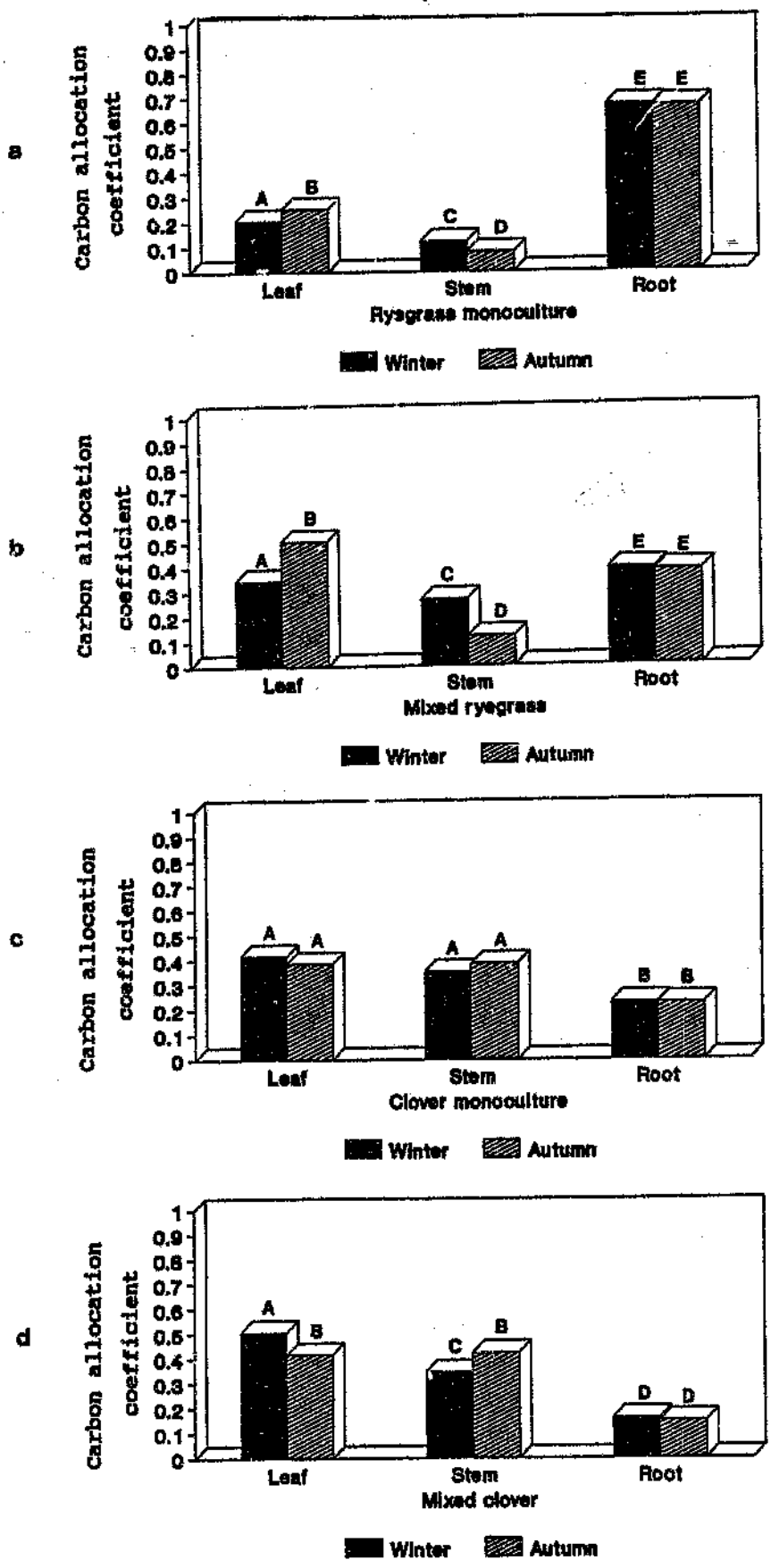
Figure 4.5. Mean growth rates of ryegrass and clover during autumn and winter.

The final point to be made about **figure 4.5.** is that the mean growth rate of the mixed clover in winter was significantly the lowest growth rate overall. This could be as a result of a number of factors, such as temperature, canopy structure and lower levels of irradiance during the winter months. The horizontal inclination of the clover leaves would be a disadvantage to the clover in the interception of irradiance entering the canopy. This problem would be accentuated during winter when there is less light entering the canopy to start with, due to lower levels of irradiance and shorter periods of daylength.

The patterns of C allocation were also shown to change (see below, **fig. 4.6**) with changes in seasons. The mixed clover had a reduced leaf C allocation during the winter, which would compound the problems experienced by the clover, resulting in the observed poor performance of this crop during the winter months.

c) Effect of temperature on the carbon allocation coefficients

A comparison of the overall C allocation patterns of ryegrass and clover (**fig. 4.6**) revealed that, in monoculture, ryegrass allocated significantly less C to leaves and stems, but significantly more C to roots, than clover. In mixture, however, the C allocation to roots of the ryegrass was significantly less than that of the ryegrass grown in monoculture, while there was significantly more leaf C allocation in mixture than in monoculture. These results suggest that the ryegrass in monoculture allocated more C to roots, enabling it to exploit soil nutrients such as nitrogen, whereas in mixture it appears that the ryegrass may be benefitting by a transfer of N from the clover thus enabling the ryegrass to allocate more C to leaves, than to roots. The resultant effect on the clover in mixture was increased shading due to the increased leaf growth of the ryegrass. This resulted in a significantly greater amount of stem C allocation in the mixed clover as compared to the clover in monoculture. These results are supported by the results of Thompson and Harper (1988), who observed that linear extension of the main axes of the clover resulted when the clover was shaded by the ryegrass.



Means with the same letter are not significantly different (Pr>F = 0.0001).

Figure 4.6. C allocation coefficients of ryegrass and clover during autumn and winter.

A comparison of carbon allocation coefficients between winter and autumn was made on ryegrass and clover, grown as both monocultures and as mixtures (fig. 4.6). Figure 4.6. shows that changes in season, from autumn to winter, had no effect on the root C allocation coefficients of either ryegrass or clover, in either monoculture or mixture. The leaf and stem C allocation coefficients of ryegrass, in both monoculture and mixture, appeared to be sensitive to the changes in season. During winter the leaf C allocation of ryegrass was significantly lower than it was during autumn, while the allocation of C to the stems was significantly higher during winter than during autumn. This suggests that during autumn the ryegrass crop had a greater leaf area index (LAI), and a lower canopy height, than during winter. This would, however, only be true if the growth rates of ryegrass were the same in winter and autumn, but since ryegrass grows at a faster growth rate during autumn the canopy height would be greater, at a specific stage of growth, than during winter.

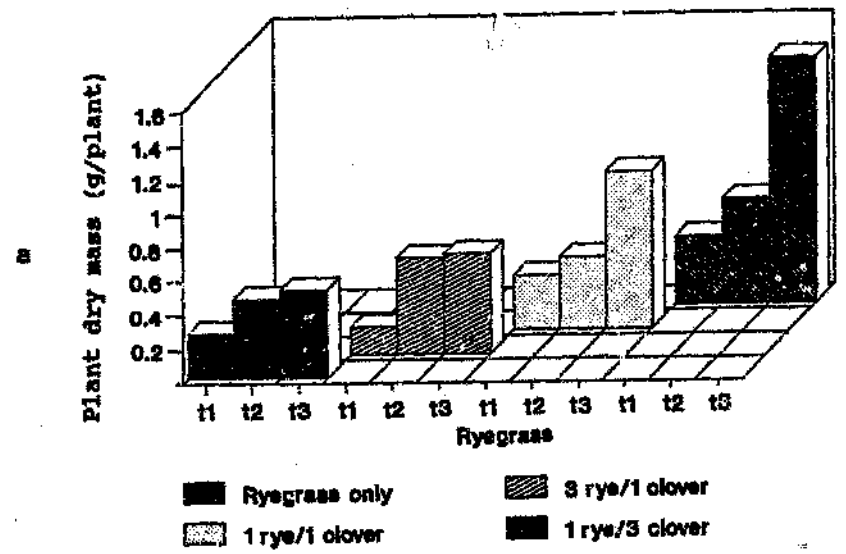
The above-mentioned changes in the leaf and stem C allocation coefficients of ryegrass were more likely to have been related to changes in irradiance levels, rather than temperature changes, associated with changes in seasons. This would explain why there were no changes in the root C allocation coefficients, of either ryegrass or clover, from autumn to winter. Also, if there was less light available then more C would be allocated to the stems, to carry the leaves closer to the light source, as was the case during winter when levels of irradiance were lower than at any other time of the year (fig. 2.3).

The clover in monoculture showed no significant differences in the allocation of C to roots, leaves, or stems, during winter and autumn. In the mixed clover sward, however, there was significantly more stem C allocation in autumn than in winter, and less leaf C allocation in autumn than in winter; i.e. the reverse of what occurred in the ryegrass. The fact that there were no changes in the C allocation coefficients in the clover monoculture, but that the mixed clover exhibited different leaf and stem C allocation coefficients in winter and autumn, indicates that changes in irradiance were responsible for affecting the C allocation coefficients, rather than changes in temperature.

In mixture, the clover gets shaded by the ryegrass so there is less light available to the mixed clover than to the clover in monoculture. Consequently, it would be expected that there would

be a greater stem C allocation, in the mixed clover, during both winter and autumn. The results, however, showed that the former was true during autumn but during winter there was a greater C allocation to the leaves with less C allocation to the stems. No explanation could be found for this result, only to say that the effect of increasing the leaf C allocation would be that the top layer of clover leaves would not necessarily receive more light, but the leaves at the bottom of the canopy would definitely be receiving less light than during autumn. This might explain why the mixed clover had such low growth rates during winter, and was subsequently outcompeted by the ryegrass.

In conclusion, it would seem that changes of temperature from autumn to winter were less likely to be responsible for any changes in C allocation coefficients than were changes in irradiance. In the case of the ryegrass the changes of irradiance appeared to have been due to changes in the seasons, while interspecific competition for light appeared to have caused the changes in the C allocation of the clover.



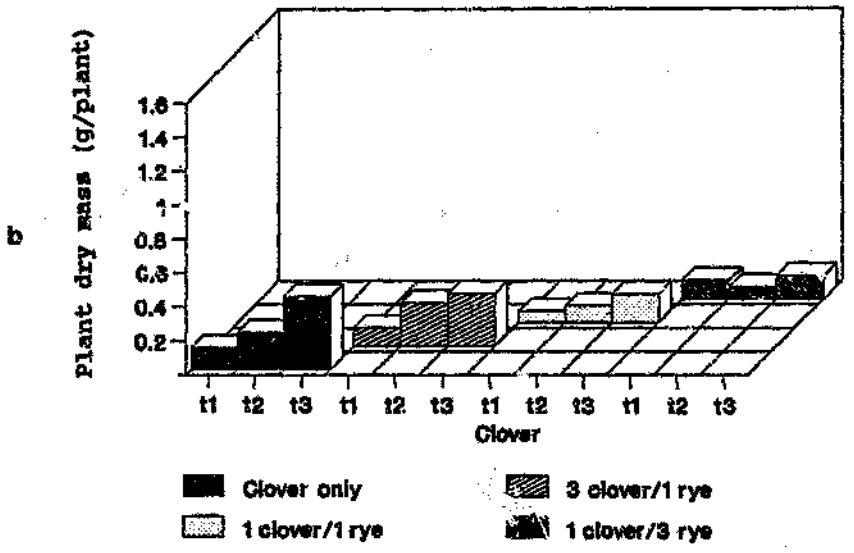


Figure 4.7. Total plant biomasses of ryegrass and clover in the interspecific competition experiment.

4.1.2. Interspecific competition experiment

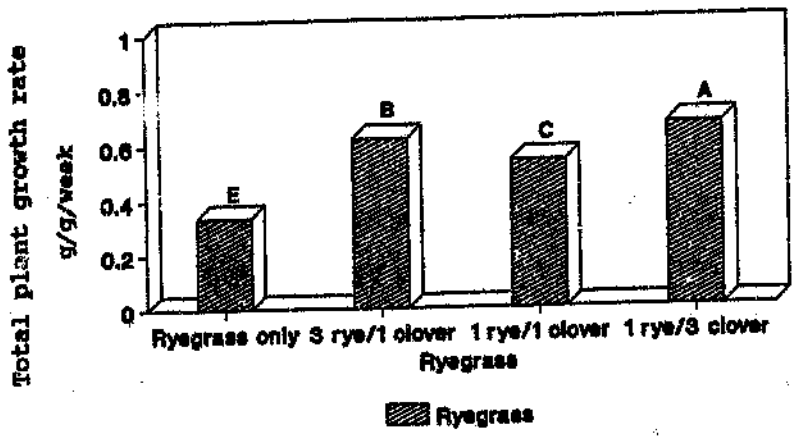
a) Effect of increasing interspecific competition on biomass and growth rates of ryegrass and clover

Ryegrass and clover were grown in mixtures of increasing interspecific proportions (but equal sowing density of 2500 seeds/m^2), as follows: ryegrass only (control);
3 ryegrass:1 clover;
1 ryegrass:1 clover;
1 ryegrass:3 clover.
And similarily for the clover:
Clover only (control);
3 clover:1 ryegrass;
1 clover:1 ryegrass;
1 clover:3 ryegrass.

Figure 4.7. represents the total plant biomasses of the ryegrass and clover components in the various mixtures, over 3 harvest periods (t1, t2, and t3) taken at 2 week intervals. **Figure 4.7(a)** clearly shows that the individual plant dry mass of the ryegrass increased as the amount of clover in the mixture was increased. The ryegrass in monoculture exhibited the least plant dry mass by the third harvest, while the ryegrass grown in the proportion 1 ryegrass:3 clover had the greatest overall plant dry mass per individual. This result indicates that ryegrass benefitted in some way from its interaction with the clover, since the more clover present, the faster the growth rate of the ryegrass. The manner in which the ryegrass benefitted from growing mixed with clover was not clear from this experiment. It was speculated that there may have been a transfer of nitrogen from the clover to the ryegrass (see next section), or that possibly the increase in the ryegrass growth may just have been a consequence of competition with the clover for resources.

The clover, on the other hand, had the most total plant dry mass per individual when grown in monoculture (fig. 4.7(b)), and this decreased successively as the amount of ryegrass in the

a



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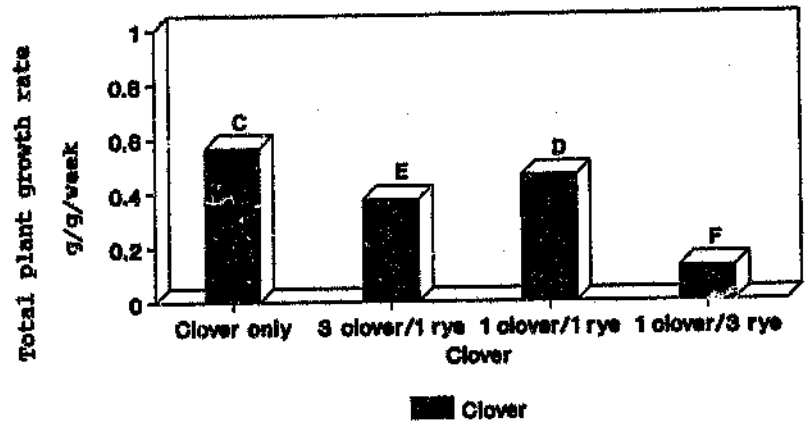

Means with the same letter are not significantly different (Pr>F = 0.0001).

Figure 4.8. Mean growth rates of ryegrass and clover in the interspecific competition experiment.

mixtures was increased. So, the benefits accrued by the ryegrass, when grown with clover, appear to have been to the detriment of the clover. This is obvious when comparing **figures 4.7(a) and 4.7(b)**, which have been drawn to the same scale, and show that the clover and ryegrass monocultures had very similar plant dry masses per individual after the third harvest, but that the clover in the proportion 1 clover: 3 ryegrass was 1/8th that of the ryegrass under the same interspecific competition.

In a mixed sward if one component grew at a faster rate than the other, then the faster growing component of the sward would soon outcompete the slower growing component. In this experiment it would appear that the growth rates of the mixed ryegrass increased as the proportion of clover was increased, resulting in increased shading of the clover and subsequent decreases in the clover growth rates. This was verified by calculating the actual growth rates of the ryegrass and clover in the various mixtures. The results **(fig. 4.8)** show that the mean growth rate of the ryegrass in monoculture was significantly lower than that of the ryegrass mixed with clover, in fact the ryegrass component of the sward containing 1 ryegrass:3 clover had a growth rate that was double that of the ryegrass in monoculture. **Figure 4.8(b)** further shows that the mean growth rate of clover in monoculture was significantly higher than that of the mixed clover, and as was expected the clover component of the 1 clover:3 ryegrass sward was the significantly slowest growing of all the combinations.

In concluding, the results of this experiment showed that ryegrass definitely benefitted from its interactions with the clover, either by a transfer of N or because of better competitive abilities than the clover, or both. The resultant effect on the clover was detrimental, probably because of increased shading of the clover by the ryegrass as the level of interspecific competition was increased.

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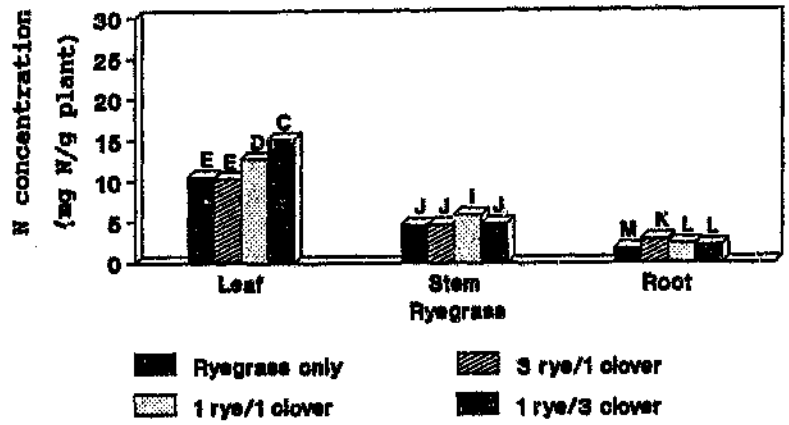

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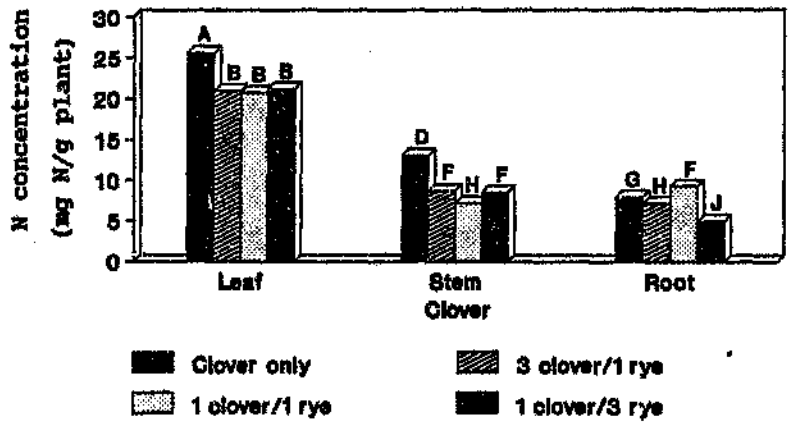


Means with the same letter are not significantly different (Pr>F = 0.0001).

Figure 4.9. N concentrations in the leaves, stems, and roots of ryegrass and clover under increasing interspecific competition.

b) Nitrogen contents of ryegrass and clover leaves, stems, and roots; in the interspecific competition experiment

Following the results of the previous experiment it seemed appropriate to determine the N concentrations in the roots, stems, and leaves of ryegrass and clover in the various mixtures. The results from such an experiment would indicate whether or not there was a transfer of N from the clover to the ryegrass.

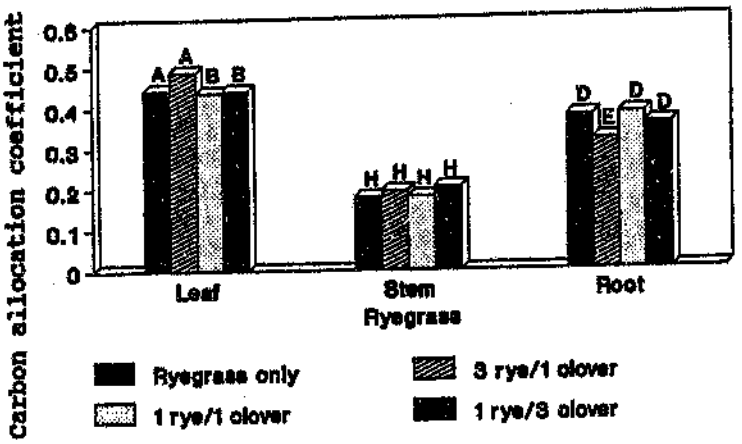
The results of this experiment (fig. 4.9) showed that clover had a higher leaf N concentration than the ryegrass. The leaf N concentrations of ryegrass and clover appear to be correlated with the single leaf photosynthetic rates of the respective crops. Ryegrass has a lower leaf N and therefore a lower single leaf photosynthetic rate relative to the clover.

The N concentration in the leaves and roots of ryegrass grown in the 1 ryegrass:3 clover combination were significanly higher than the N concentrations in ryegrass monoculture leaves and roots. In the case of the clover, however, there was a significantly higher N concentration in the leaves, stems, and roots of the clover grown in monoculture, than the N concentrations of the leaves, stems, and roots of the clover grown in the 1 clover:3 ryegrass mixture.

These results suggest that some N was indeed being transfered from the clover plants to the ryegrass plants when the two were grown together. The manner in which this transfer of N had occurred is not clear from these experiments. It could have been either a direct transfer of N, or an indirect transfer of N from decomposing clover plants, or via mycorrhizal fungi. This could only be ascertained by using labelled N in the form of ^{15}N, but this was not within the scope of this project. It is, however, more probable that a direct transfer of N occurred since the relatively short time within which this experiment was carried out would not account for long term effects of N transfer by decomposition of the clover. Transfer of N via mycorrhizal fungi is also unlikely since the clover seeds were pretreated with fungicide.

(Note: It should be noted that the clover was always nodulated, possibly as a result of *Rhizobium* existing in the soil.)

a



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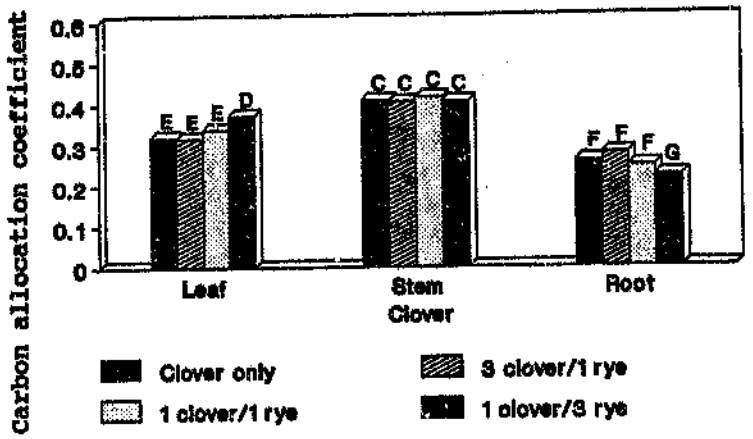


Means with the same letter are not significantly different (Pr>F = 0.0001).

Figure 4.10. C allocation coefficients of ryegrass and clover under increasing interspecific competition.

c) Effects of interspecific competition on carbon allocation coefficients of ryegrass and clover

A comparison was made of the C allocation coefficients of both ryegrass and clover, under increasing levels of interspecific competition. The results are presented in **Figure 4.10.**

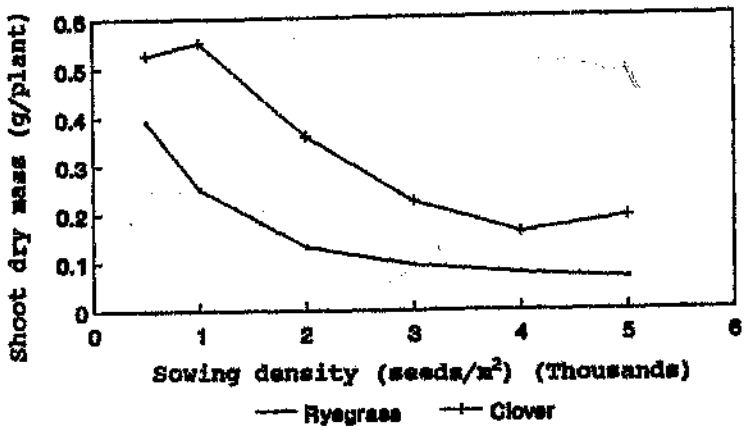
This experiment showed that the C allocation of ryegrass was not particularly sensitive to interspecific competition. This is seen in **figure 4.10(a)** where there was clearly no trend in either the leaf, stem, or root C allocations of the different mixtures.

In the case of the clover there was a clear trend of increasing leaf C allocation, and decreasing root C allocation, as the interspecific competition increased. There was no significant difference in the stem C allocation of the clover with increasing proportions of ryegrass in the mixture. The increasing leaf C allocation was probably a reaction to the reduced amounts of irradiance brought upon by the increasing presence of ryegrass within the sward. By increasing the allocation of C to the leaves, the clover would be increasing its surface for light interception, under conditions of increasing light competition.

The decreasing root C allocation of the clover, was probably due to an increase in the clover root senescence rate brought on by an increase in underground competition for space and resources.

In concluding, it would seem that ryegrass was not adversely affected by increasing interspecific competition. The fact that ryegrass grew faster, and had higher N concentrations, under increasing proportions of clover in the mixture, indicates that ryegrass benefitted from its interactions with clover. The clover, however, did not appear to benefit in any way from its interactions with ryegrass. As the proportions of ryegrass in the mixture were increased, so the growth rates and N concentrations of the clover decreased, while there was also a change in the C allocations to the leaves and roots of the clover. The different responses of the 2 crops to increasing interspecific competition were probably largely due to their different canopy structures. The vertically inclined leaves and higher canopy of the ryegrass would result in minimal interference of the ryegrass by the clover, while the horizontally inclined leaves and lower canopy height of the clover would inevitably lead to shading of the clover by the ryegrass when the two crops are grown in mixed swards. Added to this, the transfer of N from the clover to the ryegrass would boost the growth of the ryegrass to the detriment of the clover, as was apparant from the above mentioned results.

a



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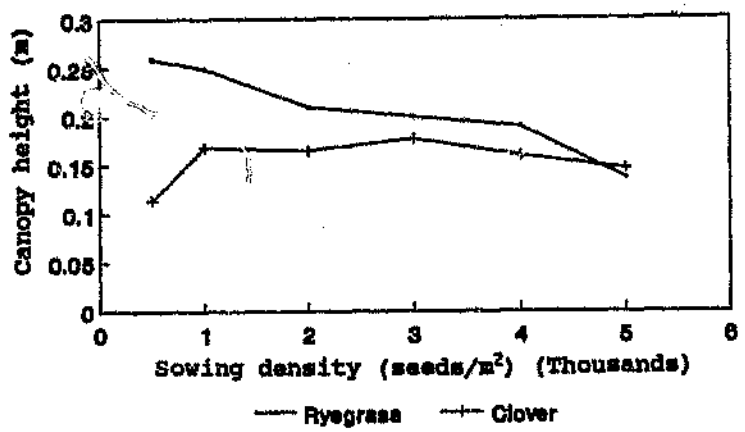


Figures 4.11 and 4.12. Effects of increasing intraspecific competition on biomass and canopy heights of ryegrass and clover.

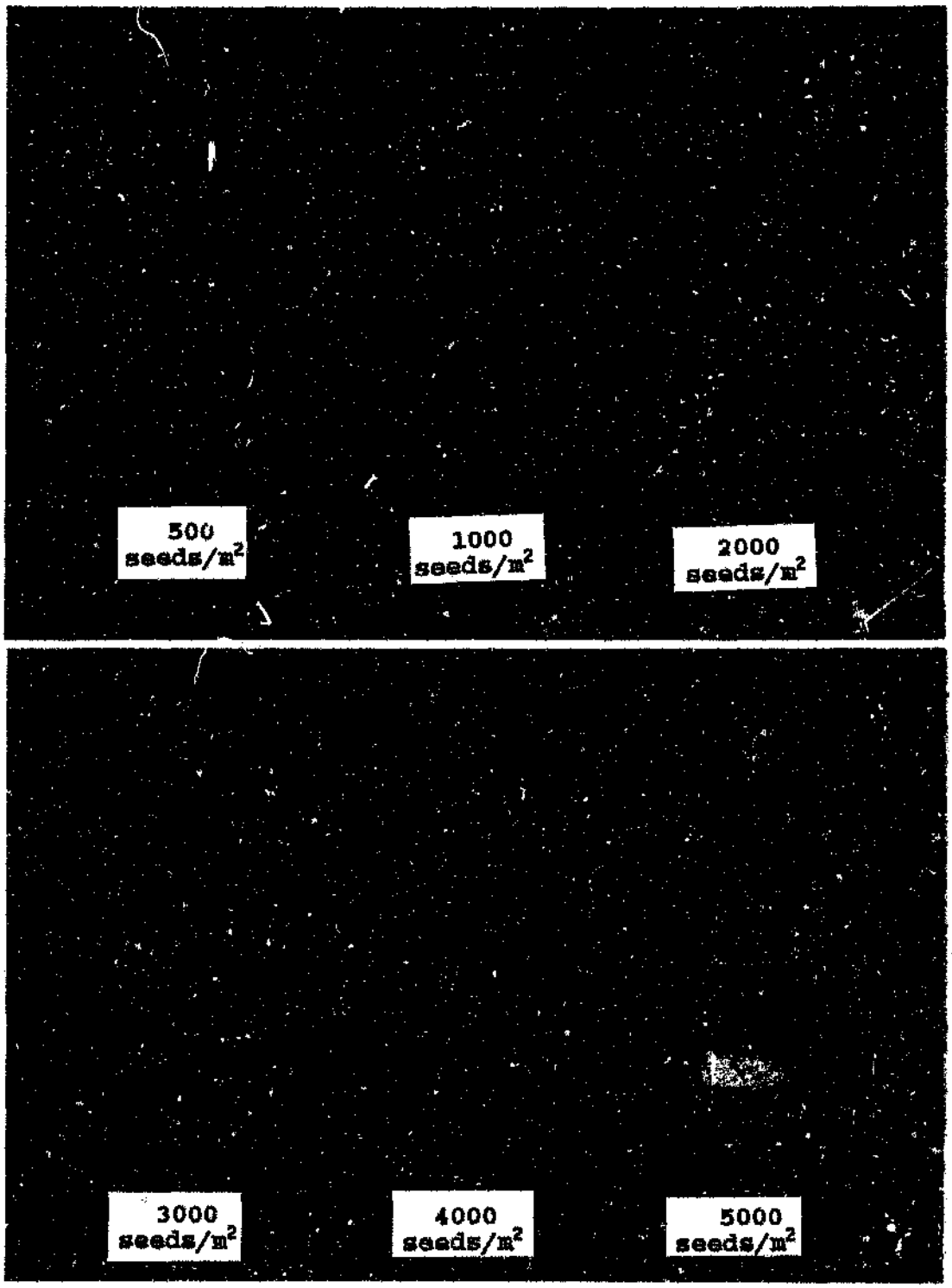


Figure 4.13. Effects of intraspecific competition on ryegrass

4.1.3. Intraspecific competition experiment

a) Effects of sowing density on yields of ryegrass and clover monocultures

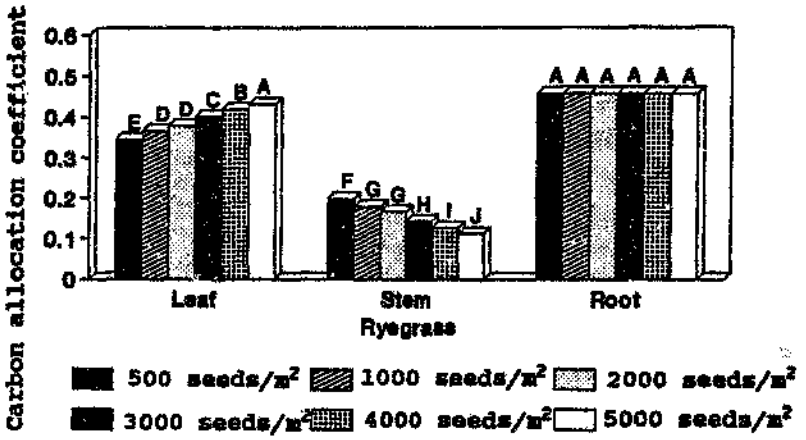
The effects of intraspecific competition at increasing densities, in terms of best yields obtained, were determined for both ryegrass and clover. Ryegrass and clover were grown as monocultures, in pots, at the following sowing densities: 500, 1000, 2000, 3000, 4000, and 5000 seeds per m^2. After ± 3 months of growth the plants were harvested and shoot biomass and canopy height were measured at each sowing density.

Figure 4.11 shows that the sowing density at which the greatest shoot biomass was obtained for ryegrass was at 500 seeds/m^2, while 1000 seeds/m^2 was the best sowing density for clover. The shoot biomasses of both ryegrass and clover decreased proportionately at densities greater than their maximal sowing densities. It is interesting to note (**fig. 4.11**) that at all densities the biomass of clover in monoculture was greater than that of the ryegrass in monoculture, at the same densities.

The maximal canopy height of ryegrass (**fig. 4.12**) was 0.26 m, at a sowing density of 500 seeds/m^2, and this decreased proportionately as the sowing density/intraspecific competition increased. This was clearly visible by merely looking at the plants (**fig. 4.13**). The same trend was not observed in the clover. The lowest canopy height, of 0.12 m, was at 500 seeds/m^2 and as density increased to 1000 seeds/m^2 the canopy height increased to 0.17 m. At densities higher than 1000 seeds/m^2, however, there was very little change in the canopy height of the clover (**fig. 4.12**).

These results indicate that ryegrass was more sensitive to increasing intraspecific competition than clover. The decreasing canopy height of the ryegrass, with increasing intraspecific competition, was probably a direct result of mutual shading. This would be verified by determining the C allocation coefficients to the various plant compartments of the ryegrass.

a



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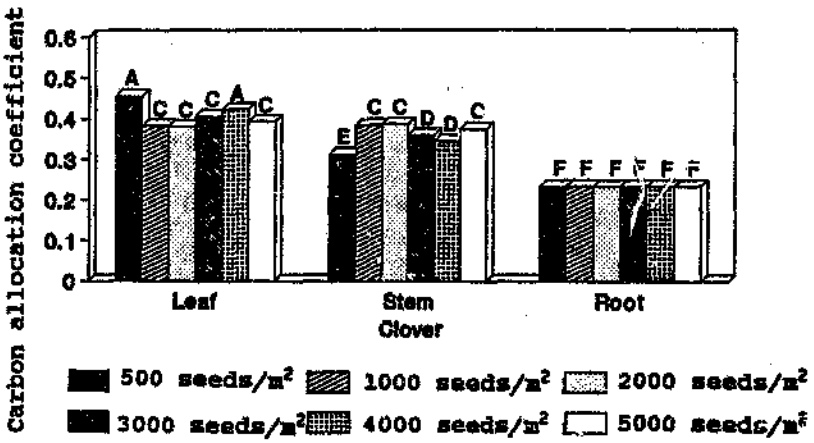

Means with the same letter are not significantly different (Pr>F = 0.0001).

Figure 4.14. C allocation coefficients of ryegrass and clover under increasing intraspecific competition.

b) Effect of density on C allocation coefficients

There was a significantly increasing proportion of leaf C allocation to the ryegrass as the density was increased (**fig. 4.14a**). This was accompanied by a significantly decreasing stem C allocation, as was expected since canopy height decreased as density increased (**figs. 4.12 and 4.13**). Density appeared to have no effect on the C allocation coefficients to the roots, stems, and leaves of the clover, since there was no significant difference of these coefficients at the different densities.

These results confirm that ryegrass was more susceptible to increasing intraspecific competition than clover. Previously it was suggested that this was due to mutual shading which is now confirmed by the fact that the root C allocation coefficients were not influenced by increasing intraspecific competition. The ryegrass plants would appear to have been competing for light, and as density increased there was less light available to each individual plant. This would explain why there was an increase in the leaf C allocation to increase the surface for light interception. From **figure 4.13** it is also evident that as density increased there was more senescent tissue than at the lower densities. This indicates that self-thinning occurred in the ryegrass at the higher sowing densities.

The reason for ryegrass being more sensitive to increases in intraspecific competition than clover, could be due to the fact that ryegrass produces tillers which would accentuate the problems of mutual shading more so than in the case of the clover.

The question arises here as to whether one can conclude that the allocation coefficients of ryegrass are flexible relative to those of the clover. The inability of clover to compete effectively may also be related to its 'fixed' or inflexibile allocation coefficients with increasing density.

Conclusions

To summarise the results of the experimental section, the following conclusions can be drawn:

1. Although the single leaf photosynthetic rates of clover were much higher than those of the ryegrass, these were not a true reflection of the observed growth rates of the respective crops within a mixed canopy. In the mixed sward, the growth rate of the ryegrass was much higher than that of the clover component. Other factors, besides single leaf photosynthetic rates, such

as quantum yield efficiency, canopy structure, ability to intercept incoming radiation, rates of respiration and senescence of the respective crops, must therefore be accounted for before an accurate prediction can be made of the performance of the 2 crops in a mixed sward.

2. The growth rates of ryegrass and clover were strongly influenced by environmental temperature, and were higher in autumn than in winter.

3. Any changes in C allocation coefficients were found to be a result of changes in the levels of irradiance. Seasonal changes in irradiance were responsible for causing changes in the C allocation coefficients of ryegrass. Changes in irradiance associated with interspecific competition for light were responsible for changes in the C allocation coefficients of the clover in mixture with ryegrass.

It also appeared that clover showed less ontogenetic drift than ryegrass, in response to increasing density and interspecfic competition.

4. Ryegrass benefitted from its interactions with clover in terms of increases in ryegrass biomass, greater growth rates, and higher N concentrations as the proportion of clover was increased within the sward. The benefit accrued by the ryegrass when grown in mixture with clover was to the detriment of the clover, resulting in decreased biomass, lower growth rates, and less N concentrations in the leaves, stems, and roots of clover as the proportion of ryegrass was increased.

5. There appeared to have been a direct transfer of N from the clover to the ryegrass.

6. Ryegrass was adversely affected by increases in intraspecific competition, contrary to the clover which appeared to be unaffected by the densities used in this experiment. The ryegrass tillers were thought to be responsible for increasing the effects of intraspecific competition in ryegrass.

4.2. MODEL OUTPUTS

The model outputs of the monoculture and mixed models for autumn and winter have been overlayed with the empirically derived data to facilitate comparison. **Figure 4.15** represents the model outputs versus the empirical data of the ryegrass (**figs. 4.15 (a) & (b)**) and clover (**figs. 4.15 (c) & (d)**) monocultures during autumn; and **figure 4.16** represents the model outputs versus empirical data of ryegrass (**figs. 4.16 (a) & (b)**) and clover (**figs. 4.16 (c) & (d)**) monocultures during winter. Total plant biomass and LAI were the two main state variables of the model and have thus been selected to represent the model outputs. The other state variables of the model are the leaf, stem, and root biomasses which are presented in table form in Appendix C. The model expresses all biomasses in units of g C/m^2, subsequently all experimental data have been converted to g C/m^2 by multiplying by 0.4 which is the conversion factor from g biomass/m^2 to g C/m^2 (Johnson & Thornley, 1985). (Means of experimental data expressed as g C/m^2 are presented in Appendix C).

Figures 4.17 and 4.18 represent the mixed crop growth models during autumn and winter, respectively. **Figures 4.17 (a) & (b)** and **4.18 (a) & (b)** represent the ryegrass component of the mixed swards, while figures **4.17 (c) & (d)** and **4.18 (c) & (d)** represent the clover component of the mixed swards.

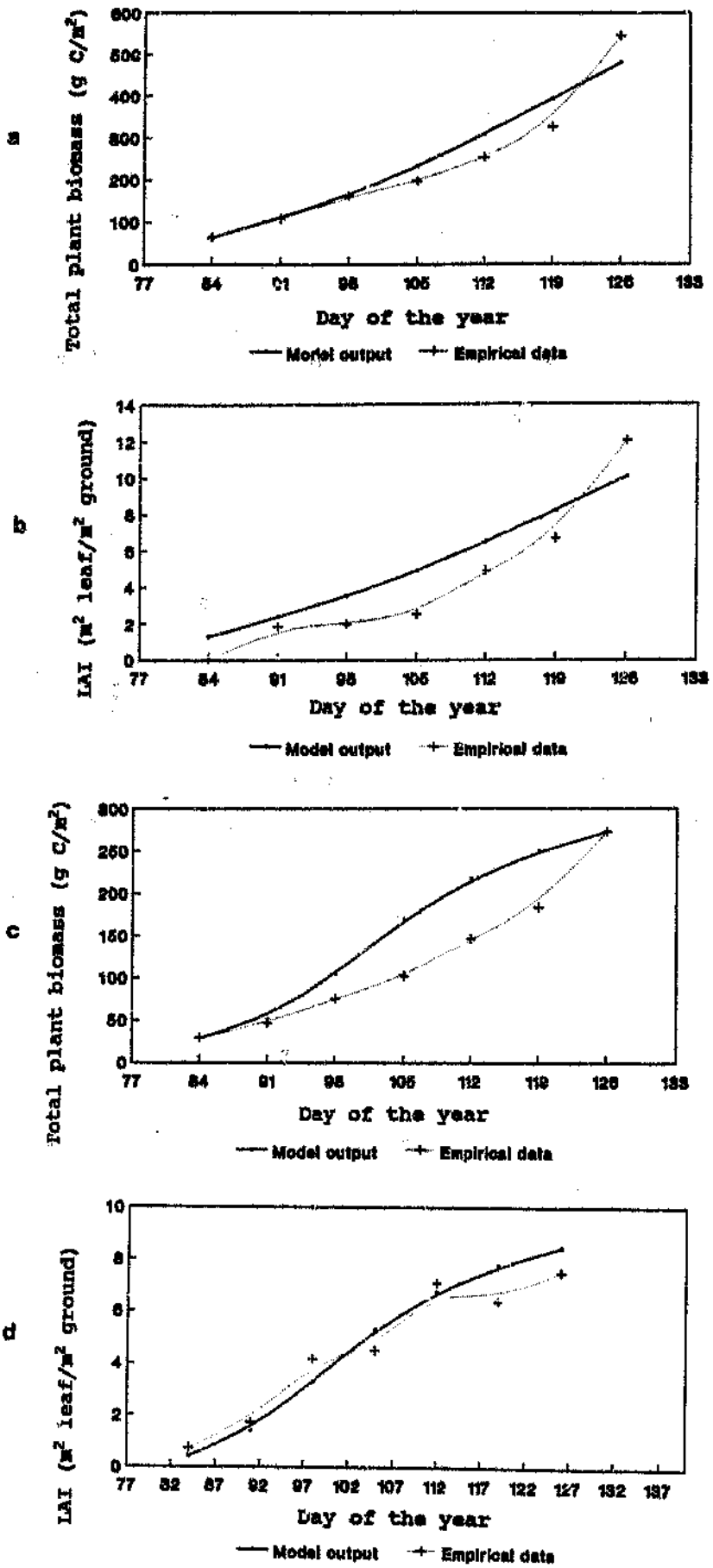

Figure 4.15. Model outputs and empirical data of monoculture crops during autumn

(Figs. 4.15 a & b = ryegrass; and Figs. 4.15 c & d = clover)

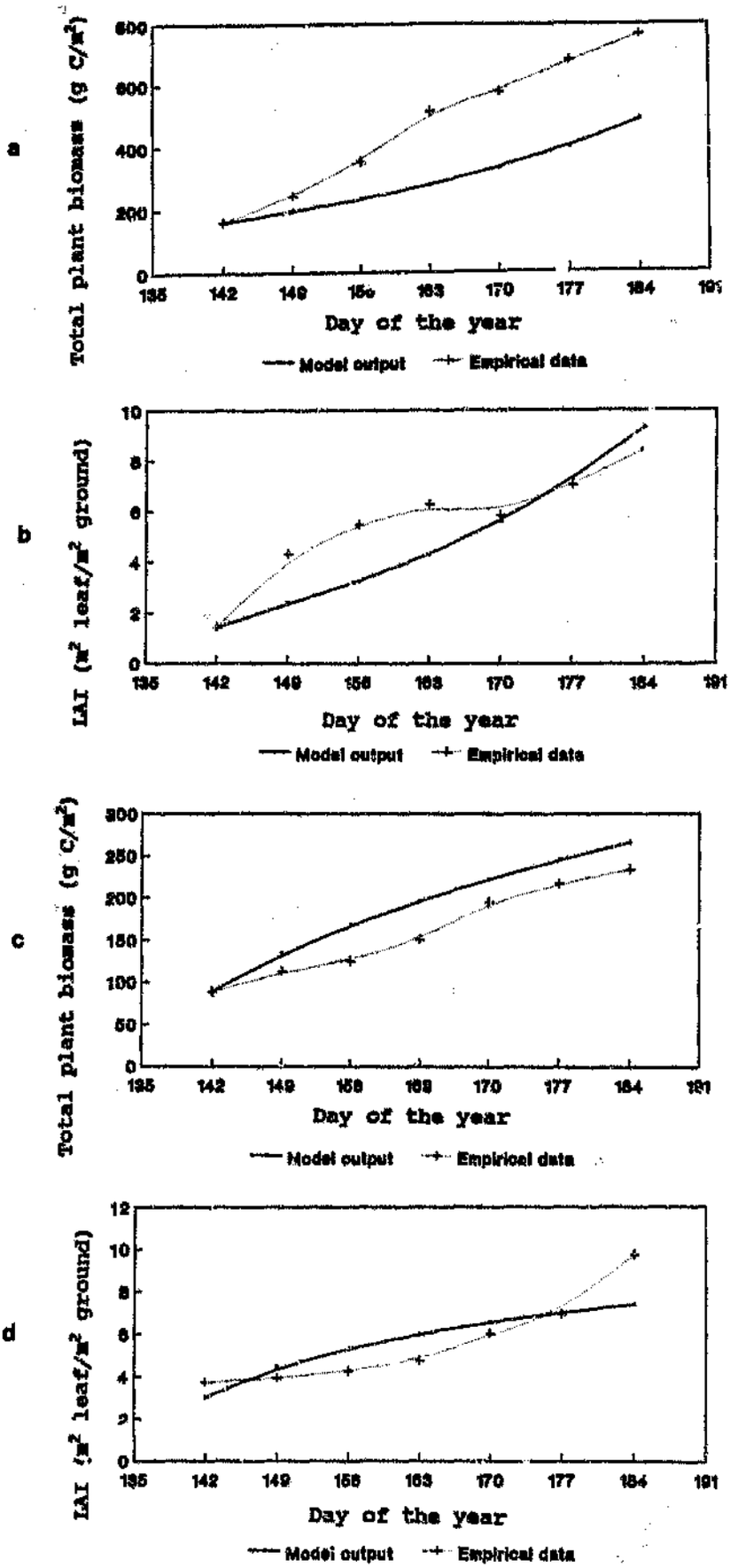

Figure 4.16. Model outputs and empirical data of monoculture crops during winter.

(Figs. 4.16 a & b = ryegrass; and Figs. 4.16 c & d = clover)

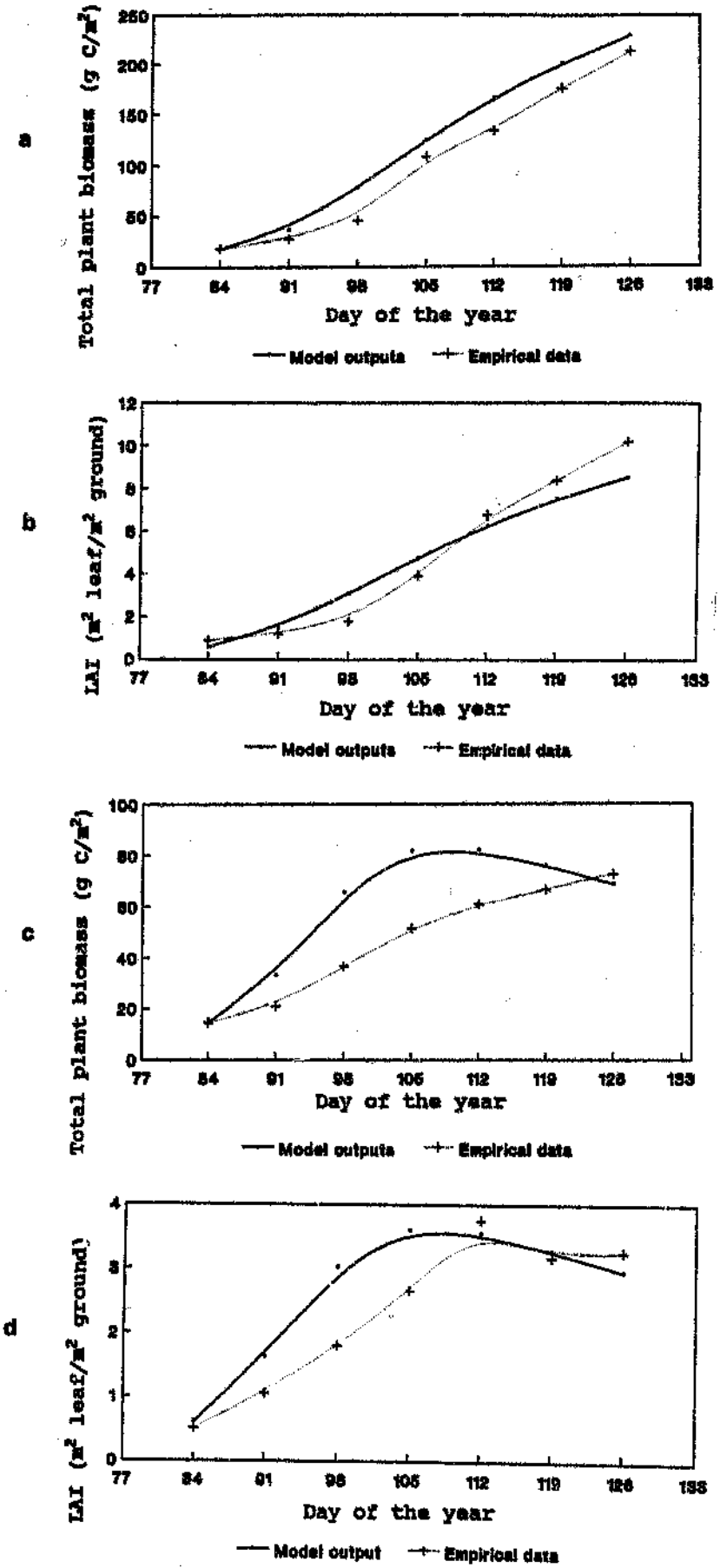

Figure 4.17. Model outputs and empirical data of mixed crops during autumn.

(Figs. 4.17 a & b = mixed ryegrass; and Figs. 4.17 c & d = mixed clover)

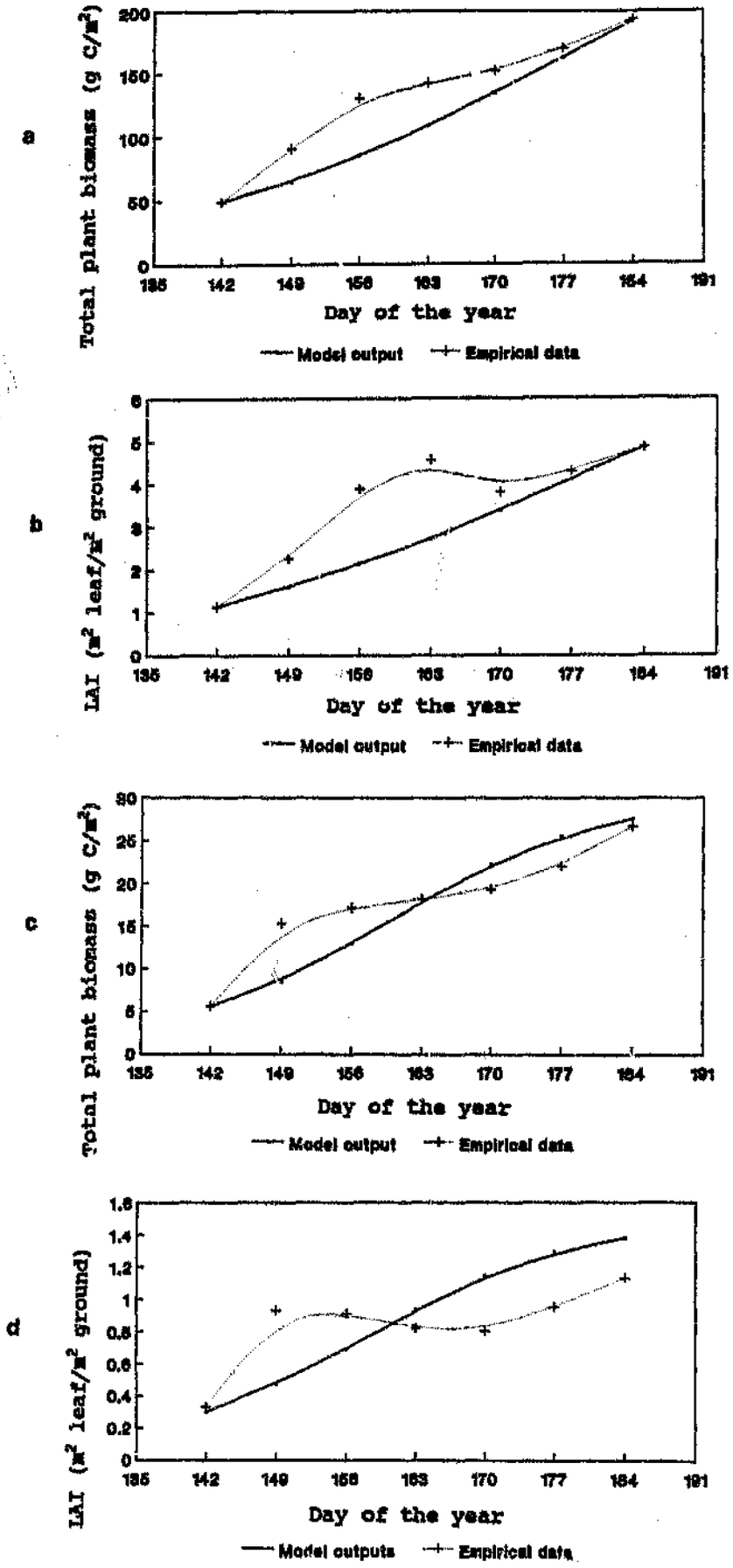

Figure 4.18. Model outputs and empirical data of mixed crops during winter.

(Figs. 4.18 a & b = mixed ryegrass; and Figs. 4.18 c & d = mixed clover)

An example of the parameters of the mixed (autumn) model follows:

Table 4.2. Parameter listing for mixed model during autumn

Parameter	Initial value	Units
Time	1	days
L1	9.34	g C/m^2
S1	2.58	g C/m^2
R1	3.96	g C/m^2
L2	6.56	g C/m^2
S2	4.40	g C/m^2
R2	3.66	g C/m^2
W1	17.87	g C/m^2
W2	14.62	g C/m^2
T	23	°C
day	38000	seconds/day
Io	100	$J/m^2/s$
X	84	day
Amax1	0.00026	g $C/m^2/s$
Amax2	0.00041	g $C/m^2/s$
A1	0.5	g $C/m^2/s$
A2	0.5	g $C/m^2/s$
LAI1	0.6	m^2 leaf/m^2 ground
LAI2	0.6	m^2 leaf/m^2 ground
*k*1	0.5	dimensionless
*k*2	0.25	dimensionless
alpha1	$1.95e^{-6}$	g C/J

Parameter (cont.)	Initial value	Units
alpha2	$1.22e^{-6}$	g C/J
X	84	day
B	6.97	dimensionless
Tm	24.9	°C
Amaxr1	0.00026	g C/m^2/s
Amaxr2	0.00041	g C/m^2/s
alphr1	0.0000033	g C/J
alphr2	0.0000024	g C/J
fs1	0.131	dimensionless
fl1	0.523	dimensionless
fr1	0.346	dimensionless
fs2	0.371	dimensionless
fl2	0.441	dimensionless
fr2	0.188	dimensionless
delta1	0.07	m^2/g C
delta2	0.1	m^2/g C
I	$1.87e^{+7}$	J/m^2/day
M1	0.025	g C/g biomass/m^2/day
M2	0.039	g C/g biomass/m^2/day
Sn1	0.1	g C/g biomass/m^2/day
Sn2	0.05	g C/g biomass/m^2/day
Y1	0.75	dimensionless
Y2	0.67	dimensionless

The initial values of biomasses and LAI in the model are taken from experimentally derived biomasses and LAI's at the first harvest. Arbitrary initial values of A1 and A2 (canopy photosynthetic rates) are used since the model calculates these from all the other photosynthetic parameters. *k*1 and *k*2 are the light penetration coefficients of ryegrass and

clover, respectively, which are 1 - the canopy extinction coefficient (k).
The carbon allocation coefficients (fs, fl, and fr) are temperature dependent, but an expression has not been derived to define this temperature dependence, so these must be changed for the winter mixed model (see Appendix C for the winter C allocation coefficients). The values of maintenance respiration and yield efficiency for ryegrass and clover have been derived from the literature (Johnson & Thornley, 1985; Mcree, 1982).

An internal sensitivity analysis was carried out on the model by adjusting the various parameters and observing the effects on the model outputs. The model was found to be sensitive to the light penetration coefficient (which is a function if canopy structure), the quantum yield efficiency, and the light saturated rate of photosynthesis, since slight changes in these parameters produced large changes in model outputs.

CHAPTER 5

DISCUSSION

5.1. Evaluation of the modelling exercise

The modelling exercise consisted of two main parts:

(1) The experimental component of the project which was essential in terms of

(a) gaining a better understanding of the competitive interactions between ryegrass and clover, and

(b) obtaining all the necessary parameters/model inputs for the model.

(2) The second part of the project was the actual modelling component which consisted of

(a) the development of the mathematical equations defining the dynamics of the system,

(b) incorporation of the experimentally derived parameters into the model, and

(c) comparison of model outputs with the empirical data.

The first experiment was designed to determine whether there was a temperature response to single leaf photosynthetic rates of ryegrass and clover. This was necessary to determine whether a temperature relationship should be incorporated into the model. The results of this experiment clearly showed that variations in temperature had a significant effect on the single leaf photosynthetic rates of both ryegrass and clover, since both Amax (the light saturated rate of photosynthesis) and α (the quantum yield efficiency) were temperature dependent (figs. 1-3). The reliability of the photosynthetic measurements was verified by the similarity of these measurements with those in the literature (Dennis & Woledge, 1982; Johnson & Thornley, 1983; 1985). The temperature dependence of Amax and α was also reported by Ehleringer & Björkman (1977), Woledge and Dennis (1982), and Johnson & Thornley (1984).

Johnson and Thornley (1983, 1984, 1985) acknowledged that an accurate prediction of photosynthesis in relation to light and temperature was necessary, since photosynthesis is the primary process in crop growth and production. They subsequently derived an expression which enabled canopy photosynthesis to be easily altered according to diurnal light and temperature fluctuations. These authors also defined Amax as being linearly related to

temperature, which according to our data was only true up to the temperature optimum above which Amax declined. Although a linear relationship between Amax and temperature may be suitable for the mild British climate, this is not appropriate for South Africa where environmental temperature often exceeds the temperature optimum for photosynthesis. Consequently we derived non-linear empirical functions to define the temperature relationships of Amax and α. These functions which fitted curves to the experimental data were used to model Amax and α rsponses to temperature.
The model is unique in that it is a mixed crop growth model which accounts for the non-linear temperature responses of both Amax and α.

The crop growth analysis experiment was carried out to determine whether the growth rates and C allocation coefficients of ryegrass and clover were temperature dependent. The accuracy of measurement of the C allocation coefficients was verified (**Table 2.1**), but the reliability of the growth rate measurements was difficult to verify due to sampling heterogeneity. This problem was also reported by Causton (1991) who found that the classical method of growth analysis, involving destructive sampling over harvest intervals, often gave misleading results due to within-sample variability. Causton (1991) suggested two alternative methods of growth analysis which were found to give much lower within-sample variability of relative growth rate than the classical method. Causton (1991) grew two batches of plants in solution culture. Fresh weights were measured non-destructively from the one batch, while the other batch was sub-sampled destructively for both fresh and dry weights. This paper came out too late to be utilized for growth rate measurements in this project.

The results of the crop growth analysis revealed that the growth rates and C allocation coefficients were temperature dependent. Although the temperature dependence of the growth rates and the C allocation coefficients were acknowledged in the model, by altering these parameters according to the season, a mathematical expression describing this relationship was not developed. The relationship between temperature and growth rate was assumed to be directly related to the temperature response of photosynthesis, which was explicitly modelled. The derivation of a temperature dependent relationship of growth rate would require extensive experimentation using more reliable methods of growth analysis (Causton, 1991) than the

classical method used in this project.

The limitations of the model included the absence of an expression describing the effects of density on growth. In the model we assumed that the initial biomass was directly dependent on density. An expression describing the self-thinning effects of density could be useful when modelling replacement series experiments in which the effects of different proportions of mixture, such as 3 ryegrass:1 clover, at high sowing densities are examined. This was not necessary in this model since a low density of 1000 seeds/m^2 was used, and a 50:50 mixture of ryegrass and clover was only modelled.

In the interspecific competition experiment it was established that ryegrass benefitted from its increased association with clover by having increased growth rates, greater canopy height, and greater N concentrations than the ryegrass in monoculture. The clover was however adversely affected by increased proportions of ryegrass in the sward. The same results were also obtained by Martin & Field (1984), Davidson & Robson (1985, 1986), Davidson et al. (1986), and Barea et al. (1989). A mathemtical expression describing the below-ground interactions (eg. N transfer) between ryegrass and clover under increasing interspecific proportions was not developed. In our model, ryegrass benefitted over clover by having a better canopy structure and higher quantum yield efficiency for light interception within a canopy. A more accurate model than the present one would include an expression describing the effects on ryegrass and clover of N transfer (from clover to ryegrass). This was not done since this would involve extensive experimental trials to establish the manner in which this N transfer occurred, and this was not an objective of this project.

Despite the above mentioned short-comings of the model, it was felt that the objectives of the modelling exercise were satisfied. The main objective of the study was to develop a mixed crop growth model of ryegrass and clover, based on the different light intercepting abilities of the two crops. This model was a synthesis of the Johnson & Thornley (1983, 1984, 1985) and the Rimmington (1984) models. The Johnson & Thornley models were all models of crop monocultures in which changing environmental factors were accounted for, while the Rimmington (1984) model was a mixed crop growth model which did not account for the

environmental fluctuations in temperature, irradiance and daylength. Rimmington's (1984) model enabled the prediction of the proportion of incident light energy absorbed by each plant component within the mixed canopy. This model provides very useful mathematical expressions of light competition since both self- and competitive shading are accounted for, but the model is not suitable for long-term predictions of yield due to the abscence of any environmentally related functions. The model accounts for the effects of a changing environment as well as including all the advantages of Rimmington's model. The model outputs were furthermore found to simulate the environmental data to our satisfaction.

5.2. Avenues for further research in this field

a) Experimental work

The problem of maintaining sufficiently large proportions of clover within mixed ryegrass/clover swards still remains. This is necessary if there is to be a constant N supply to the grass component by the clover, thus improving forage yields and reducing the costs (both monetary and as pertaining to clover) of applying N fertilizer. Although much work has already been done towards solving this problem there is still some controversy in the literature about certain potential treatments. For example, much work has been done to ascertain the responses of both ryegrass and clover to harvesting, yet different results are reported in the literature. Harvesting has been reported by some authors (Haynes, 1980; Chapman et al., 1991) to boost the performance of clover within a mixed sward, while other authors (Hartwig et al., 1987; Woledge, 1988) found that harvesting had a detrimental effect on clover and reduced its relative proportions within mixed swards. The possibiltiy exists that the stage of growth may be important in terms of the best time for harvesting. This could be tested by harvesting clover at various pre-determined stages of its development. Positive results from such an experiment could be used for better management practices and may offer the solution of maintaining clover within reasonable proportions within mixed ryegrass/clover swards.

The inoculation of clover with vesicular-arbuscular mycorrhizae has been reported by Barea et al. (1989) as necessary for the suitable development of the clover. Vesicular-arbuscular (VA) mycorrhizae enhance the ability of the host plant to absorb phosphates from the soil, and thus boost N_2-fixation which is a P-dependent process (Barea & Azcon-Aguilar, 1983). The

effects of VA mycorrhizae on the ryegrass component of the mixture need to be examined before this method can be used commercially. It is also not clear how these mycorrhizae affect the process of N transfer from clover to ryegrass, and this should also be determined. Other work that can be done is to determine the physiological association of the mycorrhizae with the clover roots to gain a better understanding of how improved P-uptake is facilitated.

Many of the reasons given for the poor competitive ability of clover in mixed swards with ryegrass have been due to the morphology of the clover. For example, Haynes (1980) isolated the horizontal inclination of clover leaves and the lower canopy height relative to ryegrass as being responsible for the poor competitive ability of clover. The position of the clover laminae within the sward, and the slow rate of leaf expansion at low temperature were considered to be the reasons for the inability of clover to maintain its proportions within the sward by Woledge (1977), Davidson & Robson (1986), Davidson et al. (1986), and Woledge et al. (1990).

All the above-mentioned reasons for the poor performance of clover tempt one to design the 'ideal' clover plant that would be morphologically capable of much better competitive abilities. Such a clover plant would have vertically inclined leaves, higher canopy with the leaves held high, and faster leaf expansion rates during winter. Such characteristics could be genetically coded for using very complicated methods of genetic engineering, or a much simpler method could be used of screening various available clover cultivars to find one that most closely resembles the 'ideal' clover plant. This approach was taken by Caradus et al. (1991) and Eagles & Othman (1989). Caradus et al. (1991) screened 158 different cultivars and breeding lines of white clover to find the one with optimal yield and persistence. They isolated a New Zealand cultivar crossed with Mediterranean germplasm as having combined attributes of both high yield and persistence. Such an experiment could be carried out to determine the best clover cultivar for the S.A. environment, since Caradus et al. (1991) found that cultivar *x* environment interaction can have a large effect on cultivar performance. Similar experiments can be carried out to isolate other attributes, such as faster leaf expansion rate at low temperature (Eagles & Othman, 1989).

The relative performance of cultivars is also affected by various management practices, such as frequency and intensity of harvesting. The screening of clover cultivars could then also be

followed by a series of other experiments (similar to those mentioned at the beginning of this section) to improve yield even further.

(b) Improving the model

The limitations of the model were discussed in section 5.1. The model could be improved by developing and incorporating the following expressions:

(1) An expression describing density dependence on growth, with self-thinning occurring at high sowing density. This should include a definition of the relationship between light attenuation and plant density, as well as an expression defining the relationship between yield and plant density. The experimental work would include determining the levels of irradiance at various strata within canopies of different sowing densities. Extensive growth analysis should also be done for the different densities.

(2) An expression should be developed to describe the N transfer from clover to ryegrass, and the resultant effects on each crop. As was already mentioned this would involve extensive experimental work to determine the process of N transfer, and the proportion of N transferred.

(3) The model could also be expanded to include a grazer. This would require some knowledge of the grazer, such as its rate of metabolism, and the amount of food needed to sustain it. The effects of urination and faecal deposition on the overall N contents would also need to be examined (Ledgard, 1991). Such a model could be valuable in determining the maximum number of grazers and the maximum grazing time which would be suitable for optimum recovery of the sward; ie. for better management practices.

(4) The temperature influence on the following expression could also be determined.

$$\left(\frac{dW}{dt}\right) = \left(\frac{dL}{dt}\right) * f_L + \left(\frac{dS}{dt}\right) * f_S + \left(\frac{dR}{dt}\right) * f_R$$

Growth rates of the various plant compartments would have to be determined using the more reliable methods suggested by Causton (1991).

A model incorporating the above-mentioned functions would be a more accurate and more comprehensive model than the model presented for this project. Considering the short-comings of this model it was found to be satisfactory in terms of meeting the objectives of the project.

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APPENDIX A

Solutions for the N determination method of Dorich and Nelson (1983)

Digestion mixture

420 ml concentrated H_2SO_4 slowly (and carefully) added to 350 ml H_2O_2 while cooling in an ice bath. Store at 2°C. Stable for 4 weeks.

Stock solution

4.719g $(NH_4)_2SO_4$ diluted to 1000 mls with de-ionized water.

Solution A

2N NaOH (sodium hydroxide 80g/l)

Solution B

12.5g EDTA (ethylene-diamine-tetra-acetic acid) in 500 ml de-ionized water adjusted to pH 10 with NaOH and 10 ml of a 0.25% methyl red solution made up in water.

Solution C

70 ml phenol and 340 mg of sodium nitroprusside in 800 ml de-ionized water. Dilute to 1000 mls.

Solution D

14.8g NaOH, 49,8g Na_2HPO_4, and 200 ml commercial bleach (sodium hypochloride 5% 50g chlorine, analytical g[illegible] from SAARCHEM). Make up to 1000 mls.

APPENDIX B

Amax and α of clover at different temperatures

Temperature	Amax ($\mu molCO_2/m^2/s$)	α ($\mu mol\ CO_2/\mu E$)
5°C	7.97	0.0279
10°C	14.01	0.0359
15°C	27.08	0.0424
20°C	34.53	0.0438
25°C	32.18	0.0492
30°C	24.32	0.0319
35°C	18.44	0.0240

Amax and α of ryegrass at different temperatures

Temperature	Amax ($\mu molCO_2/m^2/s$)	α ($\mu molCO_2/\mu E$)
20°C	14.38	0.0665
25°C	15.61	0.0431
30°C	23.67	0.0345
35°C	13.26	0.0564

APPENDIX C

Mean experimental data for ryegrass monoculture during winter

X1	W	L	S	R	LAI
142	159.06	28.80	19.20	111.06	1.41
149	243.89	36.64	35.96	170.29	4.32
156	349.90	64.94	40.66	244.30	5.47
163	514.25	100.88	54.32	359.05	6.30
170	576.53	106.84	67.16	402.57	5.86
177	682.27	133.90	72.10	476.57	7.06
184	766.07	150.28	80.92	534.87	8.45

Model outputs for ryegrass monoculture during winter

X1	W	L	S	R	LAI
142	159.06	28.80	19.20	111.06	1.40
149	195.60	36.64	24.14	139.46	2.37
156	231.37	43.68	28.57	164.93	3.25
163	276.11	52.46	34.11	196.76	4.31
170	331.65	63.36	40.98	236.27	5.63
177	400.67	76.90	49.53	285.41	7.28
184	487.08	93.89	60.25	347.03	9.34

(Note: All biomasses are expressed in g C/m^2.)

Mean experimental data for clover monoculture during winter

X1	W	L	S	R	LAI
142	88.61	36.77	31.23	20.61	3.73
149	112.58	47.67	33.13	24.49	3.92
156	124.85	58.53	35.87	30.45	4.24
163	150.84	61.22	52.75	36.84	4.74
170	194.93	80.78	68.82	45.34	5.89
177	217.34	85.07	81.73	50.55	6.94
184	234.0	90.17	86.63	57.20	9.74

Model outputs for clover monoculture during winter

X1	W	L	S	R	LAI
142	88.61	36.77	31.23	20.61	3.0
149	133.76	61.32	46.16	31.32	4.44
156	167.29	79.15	54.94	37.65	5.29
163	196.70	95.61	62.14	42.84	5.98
170	222.51	110.85	68.02	47.08	6.55
177	245.48	125.15	72.84	50.57	7.01
184	266.31	138.82	76.85	53.48	7.40

Mean experimental data for mixed ryegrass during winter

X1	W	L	S	R	LAI
142	48.96	12.0	18.40	18.56	1.14
149	90.84	25.94	30.46	34.44	2.26
156	130.14	53.81	26.99	49.34	3.89
163	141.94	54.28	33.84	53.82	4.56
170	152.05	50.98	43.42	57.65	3.81
177	170.0	57.68	48.40	65.68	4.30
184	193.93	65.02	55.38	73.33	4.86

Model outputs for mixed ryegrass during winter

X1	W	L	S	R	LAI
142	48.96	12.0	18.40	18.56	1.14
149	64.71	18.43	23.42	25.55	1.61
156	84.93	25.57	29.12	33.38	2.13
163	108.23	33.69	35.74	42.38	2.72
170	134.28	42.68	43.14	52.38	3.39
177	162.62	52.40	51.20	63.23	4.11
184	192.84	62.71	59.80	74.77	4.87

Mean experimental data for mixed clover during winter

X1	W	L	S	R	LAI
142	5.62	2.95	1.55	1.12	0.33
149	15.34	8.70	4.65	3.32	0.93
156	17.12	9.74	5.16	2.22	0.91
163	18.18	9.42	6.41	2.36	0.82
170	119.29	9.74	6.66	2.89	0.80
177	22.0	11.78	8.10	3.14	0.95
184	26.68	13.79	9.43	3.46	1.13

Model outputs for mixed clover during winter

X1	W	L	S	R	LAI
142	5.62	2.95	1.55	1.12	0.30
149	8.47	4.80	2.72	1.56	0.47
156	13.02	7.28	4.27	2.16	0.69
163	17.85	9.86	5.87	2.78	0.93
170	22.21	12.13	7.29	3.33	1.14
177	25.53	13.81	8.34	3.74	1.29
184	27.55	14.80	8.97	3.97	1.38

Mean experimental data for ryegrass monoculture during autumn

X1	W	L	S	R	LAI
84	63.91	15.33	3.96	44.62	1.32
91	108.34	26.20	6.50	75.64	1.86
98	161.19	34.37	14.26	112.55	1.97
105	196.15	45.84	13.36	136.95	2.54
112	251.83	58.66	17.24	175.83	4.90
119	325.58	75.86	22.40	227.32	6.67
126	545.28	124.54	40.02	380.71	11.99

Model outputs for ryegrass monoculture during autumn

X1	W	L	S	R	LAI
84	63.91	15.33	3.96	44.62	1.30
91	110.16	28.02	7.99	81.06	2.38
98	164.18	41.36	12.21	119.39	3.51
105	230.75	57.65	17.34	166.19	4.89
112	307.79	76.34	23.22	219.91	6.49
119	392.14	96.66	29.60	278.31	8.21
126	480.20	117.75	36.21	338.91	10.01

Mean experimental data for clover monoculture during autumn

X1	W	L	S	R	LAI
84	28.90	9.24	4.52	15.13	0.72
91	46.94	14.40	8.83	23.70	1.72
98	75.40	38.19	19.68	17.54	4.16
105	102.19	41.64	36.78	23.76	4.51
112	145.96	52.0	57.47	36.49	7.11
119	183.18	63.12	77.46	42.60	6.41
126	272.84	87.19	122.20	63.45	7.52

Model outputs for clover monoculture during autumn

X1	W	L	S	R	LAI
84	28.90	9.24	4.52	15.13	0.40
91	50.93	20.61	17.07	19.06	1.39
98	105.23	43.56	40.83	30.30	3.29
105	168.80	68.01	65.85	42.90	5.28
112	216.93	86.01	84.26	52.20	6.75
119	250.0	98.35	96.89	58.54	7.76
126	272.60	106.79	105.56	62.83	8.45

Mean experimental data for mixed ryegrass during autumn

X1	W	L	S	R	LAI
84	17.87	9.34	2.58	5.96	0.89
91	27.49	14.89	3.42	9.16	1.19
98	45.21	24.22	5.92	15.07	1.80
105	107.66	57.97	13.21	36.48	3.93
112	133.60	70.80	17.11	45.69	6.78
119	175.62	87.50	22.74	65.37	8.38
126	213.84	106.57	28.54	78.73	10.20

Model outputs for mixed ryegrass during autumn

X1	W	L	S	R	LAI
84	17.87	9.34	2.58	5.96	0.60
91	36.92	21.84	5.64	14.28	1.49
98	77.87	44.25	11.21	29.15	3.07
105	124.69	68.53	17.27	45.24	4.77
112	166.17	89.71	22.55	59.27	6.26
119	200.91	107.41	26.97	70.99	7.50
126	229.84	122.15	30.65	80.76	8.54

Mean experimental data for mixed clover during autumn

X1	W	L	S	R	LAI
84	14.62	6.56	4.41	3.66	0.51
91	20.90	9.30	6.95	4.64	1.05
98	36.67	17.81	12.19	6.67	1.80
105	51.54	23.43	20.39	7.72	2.66
112	60.92	26.16	26.05	8.70	3.75
119	66.53	28.28	27.16	11.09	3.18
126	72.62	29.02	28.79	14.82	3.26

Model outputs for mixed clover during autumn

X1	W	L	S	R	LAI
84	14.62	6.56	4.40	3.66	0.60
91	33.25	16.83	13.20	7.91	1.63
98	65.74	30.67	24.97	13.72	3.03
105	81.73	36.43	29.92	16.10	3.61
112	81.84	35.88	29.53	15.80	3.55
119	75.91	33.09	27.25	14.56	3.28
126	68.71	29.91	24.62	13.16	2.96

Mean carbon allocation coefficients

Ryegrass monoculture

Season	f_L	f_S	f_R
Winter	0.187	0.117	0.696
Autumn	0.237	0.075	0.688

Mixed ryegrass

Season	f_L	f_S	f_R
Winter	0.333	0.288	0.379
Autumn	0.523	0.131	0.346

Clover monoculture

Season	f_L	f_S	f_R
Winter	0.421	0.339	0.240
Autumn	0.393	0.387	0.220

Mixed clover

Season	f_L	f_S	f_R
Winter	0.535	0.331	0.134
Autumn	0.441	0.371	0.188

APPENDIX D

To integrate

$$A = \frac{Amax * \alpha I_o}{Amax + \alpha I_o}$$

which is a single leaf relation over the entire canopy we need to consider the following: (i) the light received by the leaf within the canopy, given by:

$$I = I_o * \exp(-k*LAI)$$

and, (ii) the photosynthesis of that leaf, given by:

$$A = \frac{Amax\ \alpha\ I_o \exp(-k*LAI)}{Amax + \alpha I_o \exp(-k*LAI)}$$

It follows from this that A for the entire canopy involves the following integration:

$$A = \int \frac{Amax\ \alpha\ I_o \exp(-k*LAI)}{Amax + \alpha\ I_o \exp(-kLAI)}\ dL$$

where dL is the variable of integration.

In order to simplify the above integral, let :

a = Amax

b = αI_o

and, u = $e^{-k(LAI)}$.

Differentiation of u = $e^{-k(LAI)}$ with respect to L gives:

$$\frac{du}{dL} = -ku$$

Therefore,

$$dL = -\frac{du}{ku}$$

$$A = \int \frac{a\,b\,u}{(a + b\,u)} \left(-\frac{du}{uk}\right)$$

or,

$$A = \int \frac{a\,b\,u}{(a + b\,u)} \frac{du}{uk}$$

$$A = \int \frac{ab}{k} \frac{1}{(a + bu)}\, du = \frac{ab}{k} \int \frac{1}{(a + bu)}\, du$$

$$\int \frac{1}{(a + bu)}\, du = \frac{1}{b} \ln\,(a + bu)$$

Therefore:

$$A = \frac{a}{k} \ln\,(a + bu)$$

We need to integrate between u = 1 and $u = e^{-k(LAI)}$, hence:

$$A = \frac{a}{k} \ln\,(a + bu)$$

Which gives:

$$A = \frac{a}{k} \ln\,[\frac{a + b}{a + bu}]$$

or,

Please note that the variable of integration is u = exp(-kLAI), therefore the limits of

$$A = \frac{Amax}{k} \ln \left[\frac{Amax + \alpha I_o}{Amax + \alpha I_o \exp(-k(LAI)} \right]$$

integration are from 1 to exp(-kLAI) if du is negative and the limits of integration are from exp(-kLAI) to 1 if du is positive, hence the meaning of sign change with respect to the variable of integration.