1. INTRODUCTION

Pinus patula Schl. et Cham., is a tree species of Mexican origin with a restricted natural distribution in the temperate to cooler temperate humid regions of south-central Mexico. In these regions, the altitude ranges between 2300 to 2700 metres above sea level, and the mean annual rainfall from 1000 to 1350 mm. Rain falls predominantly in the summer months. *P. patula* was introduced into South Africa in 1907 by Sir David Hutchins. In South Africa, the species grows best on cool, moist sites in the summer rainfall region. It is planted on the humid seaward slopes of the escarpment and foothills from the Eastern Cape to the Northern Province. It also grows well against the slopes of the higher coastal ranges and more humid parts of the interior plateau. The greater part of the area where it grows in South Africa lies between 900 and 1800 metres above sea level.

P. patula is the most important softwood plantation tree species grown in South Africa. Softwood species occupy approximately 31% of the total area under commercial plantations, of which 246 000 ha (42%) is *P. patula* (Anon. 1988). Detailed descriptions of *P. patula*, its silviculture and site requirements are given by Loock 1950, Poynton 1979, Schutz and Schafer (1985), Schonau and Grey (1987) and Perry (1991). Growth in the demand for softwoods is projected at 3.5% per annum. It is estimated that softwood will increase its share of the total roundwood market from the current 42% to 54% by the year 2010. The forecast demand for softwood by 2010 will be approximately 15.8 million cubic metres (van der Zel 1989). This increase in demand will place tremendous pressure on land acquisition for afforestation. However, due to the shortage of suitable land as well as increasing environmental pressure on potential afforestable areas, these requirements cannot be met solely through increased afforestation. The shortfall in demand will have to be met by maximizing yield on existing sites. This can be achieved by instituting sound silvicultural practices such as the utilization of genetically improved seed, fertilizer application and reduction in weed competition.

Setaria megaphylla (Steud.) Dur and Schinz, also known as ribbon bristle grass is an indigenous grass which has become a weed in plantations throughout the summer rainfall region of southern Africa. It occurs at medium to low altitudes, throughout tropical and parts of sub-tropical Africa (Chippindall and Crook 1976). It is perennial and occurs in shady, moist habitats as well as in the open in higher rainfall areas. *S. megaphylla* grows in the form of a dense tussock. It is easily recognised by its leaves, which are pleated and up to 1.5 m in length and 100 mm wide. Detailed descriptions of the plant are given by Chippindall and Crook (1976) and Clayton and Renvoize (1982).

In a survey carried out by van Heerden and Masson (1991), of weed species in newly regenerated pine plantations in the Mpumalanga and the Northern Province, *S. megaphylla* was found to be one of the most widely distributed species. A strong correlation was found between altitude and the incidence of

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ABSTRACT

Christie, S.I., 1994. The effect of the grass *Setaria megaphylla* on the growth of *Pinus patula*. Ph.D Thesis, University of Witwatersrand, Johannesburg, South Africa.

A three-year study was undertaken in the province of Mpumalanga, South Africa to investigate the competitive effects of the grass *Setaria megaphylla* on the growth of the tree species *Pinus patula*. A replacement series field trial, where six different competition regimes were implemented, clearly demonstrated the suppressive effects of *S. megaphylla* on the growth of *P. patula*. Compared to trees growing under high competition regimes, height, root collar diameter and volume index for *P. patula* after three years was respectively 35, 44 and 80% greater for low regimes. This competitive effect was reflected in other growth parameters such as needle length, biomass, root length and root configuration. The study demonstrated the dynamics of carbon allocation to the various biomass components of *P. patula* growing under different competition regimes. The relative growth rates of *P. patula* provided insight into the transition from inter to intraspecific competition. The possible causal effects of competition were also investigated. For *P. patula* there was an inverse relationship between the level of competition and light-use efficiency. Studies of soil moisture content, plant water potential, water stress integral and water balance provided strong evidence that competition for water was the most limiting factor in the early growth of *P. patula*. In the nutrient studies, vector analyses supported the hypotheses that competition between *P. patula* and *S. megaphylla* for water limited the growth of *P. patula*.

Keywords: *P. patula*, *S. megaphylla*, competition, weed, water, stress, potential, nutrient light.

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I dedicate this dissertation to my Parents.

DECLARATION

I declare that the results contained in this thesis are from my own original work except where acknowledged.

S.I. Christie
December 1995

THE EFFECT OF THE GRASS SETARIA MEGAPHYLLA ON THE GROWTH OF PINUS PATULA.

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Submitted in partial fulfilment of the requirements
for the degree of *Doctor of Philosophy*

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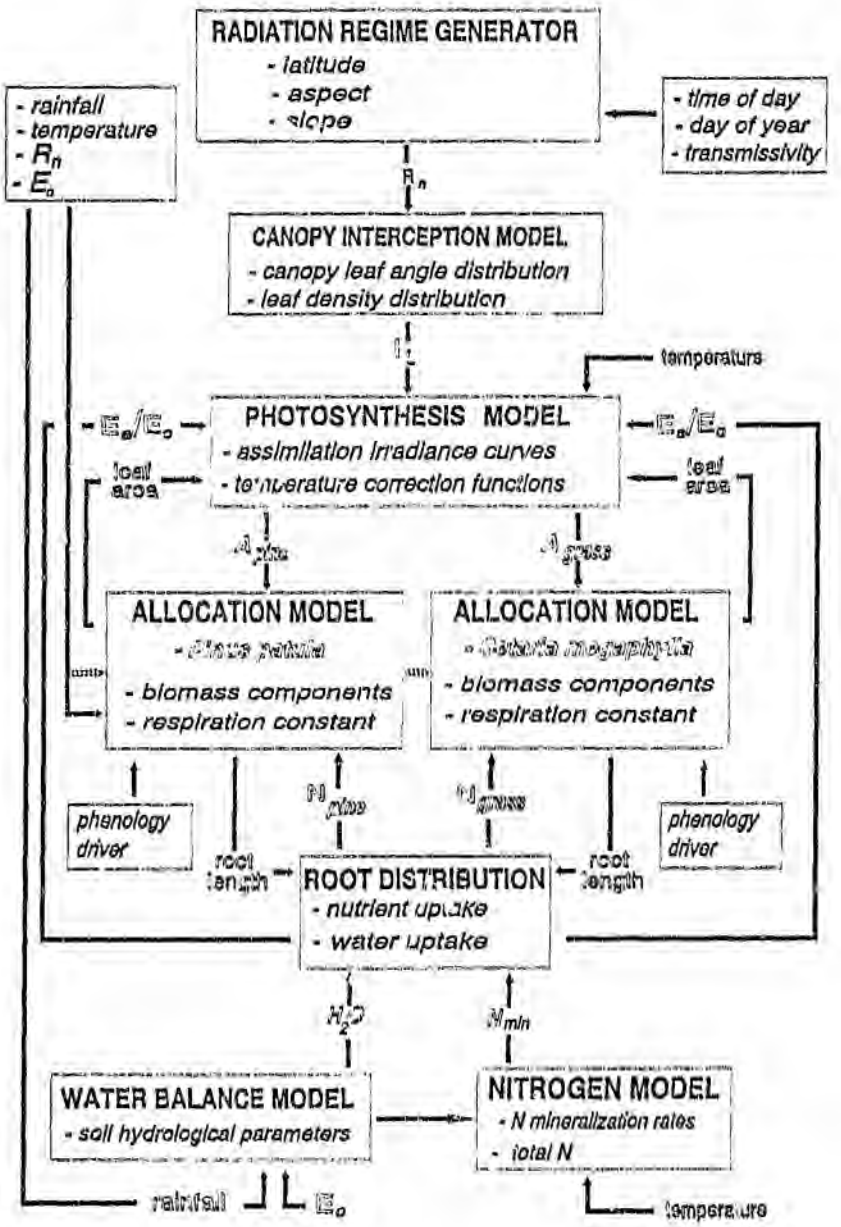

Figure 2.2. A flow diagram illustrating the conceptual structure of a model of the competitive interaction between *P. patula* and *S. megaphylla*.

It should be remembered that, process-based models are intended primarily as research tools. These models usually consist of submodels with each submodel describing a different process. A schematic diagram depicting the sub-components or submodels of a competition model is shown in Figure 2.2. Simulation models should be constructed in such a way that parameters are few enough to be measured directly or indirectly. This involves dealing with only two of the subsystems of the tree crop at a time, and exploring the interactions between them. The objective of such a model would be to predict the product of the two subsystems. If this fails, then one can re-evaluate the hypotheses (Passioura 1973).

2.3 The effect of competition on the growth and survival of *Pinus* species

Much of the work on competition has been carried out under controlled conditions in the laboratory (Harper 1961, Gause 1971). In the field it is often difficult to separate the factors involved in competition from other possible causes of negative correlation. Connell (1983), surveyed the prevalence and relative importance of interspecific competition in field experiments. The survey was restricted to the years, 1972 to 1982, in six ecological journals. This survey yielded 72 papers including 215 species with 527 field experiments. 93% of the investigations involving single species recorded competition.

In a survey carried out by Schoener (1983) of experimental data to detect interspecific competition in the field, 148 of the 164 studies, or 90%, claimed to have detected competition. With regard to studies of terrestrial plants and mechanisms of competition, 28 were consumptive, 3 pre-emptive, 11 overgrowth and 7 interference. Both these surveys indicated that many of the experiments carried out may be fundamentally flawed with respect to the detection, degree and mechanisms of competition. The surveys also illustrate the difficulty in producing clear and unambiguous demonstrations of interspecific competition.

The adverse effects of weed competition on the early growth and survival of plantation trees has been well demonstrated. Stewart *et al.* (1987) have described over 200 studies which show that vegetation manipulation improves tree growth and survival. These studies reported stand-volume increases of 40 to 100% when competing vegetation was controlled. The increases in tree growth were found to be related to the degree of weed control despite a wide range of conifer species, weed types, stand conditions, environments and control methods (Wagner *et al.* 1989). A number of examples pertaining to pines are given below.

Yield tables and descriptive statistical growth models of plantation yield, which are of great value to practical forest management, are usually unsuitable for investigating particular aspects of tree growth. Inaccurate yield predictions also result when these models are used in situations outside the range of data on which they are based. In addition, as soon as management interventions that change growing conditions are instituted, growth projections based on descriptive yield models become unreliable. Examples of management interventions include weed control, fertilizer application and site preparation. In order to improve reliability, attempts have been made to incorporate biological aspects of forest growth into statistical models and yield tables, or to base the choice for any particular descriptive model on a general notation of biological phenomena (Pienaar and Turnbull 1973). As early as the mid-19th century, the inflexibility of the negative hyperbolic or historical-bioassay approach caused some German mensurationists to conclude that yield prediction should be based on an understanding of the determinants of forest growth (Kimmins *et al.* 1990). By the early 1970's this philosophy had led to the development of process-based simulation models of forest growth (Kimmins *et al.* 1990). McMurtrie and Wolf (1980) and McMurtrie *et al.* (1990) cite a number of researchers who have developed process-based growth models of tree or stand growth.

A process-based model for crop-weed competition was introduced by Spitters and Aerts (1983), in which competition effects are separated from the underlying processes. This approach is based on the distribution of the growth-determinants and limiting resources of light, water and nutrients between the species. The formation of dry matter by the species is computed from the amount of resources (light, water or nutrients) acquired by the competing species, and the efficiency of the species in using these resources (Kropff 1988). Kropff and Spitters (1992) used this process-based approach to develop an interspecific competition model between weeds and sugar beet.

Process-based models have been developed for situations where water and/or nutrients are limiting tree growth (Mohrens 1987; Kimmins *et al.* 1990; McMurtrie *et al.* 1990). A comprehensive multidisciplinary field experiment studying the effects of water and nutrients on the growth of *P. radiata* led to the development of a detailed process-based model of tree growth (McMurtrie and Landsberg 1992). Conditions for the co-existence of trees and grass using a mathematical model describing plant competition for radiation, water and nutrients are given by McMurtrie and Wolf (1983). These models may be useful in gaining a more thorough insight into the tree-weed system. The advantage of the process-based approach is that the resultant model, if thoroughly validated, can be used to analyze competition effects in untried situations, since the model is valid for a large range of environmental conditions (Kropff 1988). However, many process-based simulation models fail to represent explicitly all significant determinants of plantation growth. They are therefore not appropriate for all situations. In order to improve the long-term predictive ability of process-based models we need to improve the extent to which they explicitly represent all the major determinants of ecosystem function.

which need to be developed for both agricultural and forest crops (Radosevich and Holt 1984, Walstad and Kuch 1987). Establishing these thresholds, however, is a difficult task that requires the ability to make several complex biological and economic predictions (Wagner *et al.* 1989). In contrast to insects and pathogens that attack crops in epidemic cycles, weeds are always present because they regenerate vegetatively or from seeds (Strelbig *et al.* 1989). The most difficult prediction is assessing the effect that the weed population will have on the crop (Walstad and Kuch 1987). However, the general applicability of these descriptive regression models is limited because they only describe the effects observed in field conditions (Kropf 1988). They describe the relationship between tree performance and a measure of interspecific competition only after losses in tree growth and survival have occurred.

Figure 2.1 illustrates a hypothetical model of the relationships between the maximum- and minimum-*response thresholds for conifer survival and growth. The maximum- and minimum- response thresholds* for tree survival and growth occur at different levels of interspecific competition. The maximum return on investment occurs when the difference between the value of production (B) and the total cost of weed control (C) is greatest. When the cost of controlling competition is equivalent to the total value of production, a 'break even' point is achieved (Wagner *et al.* 1989).

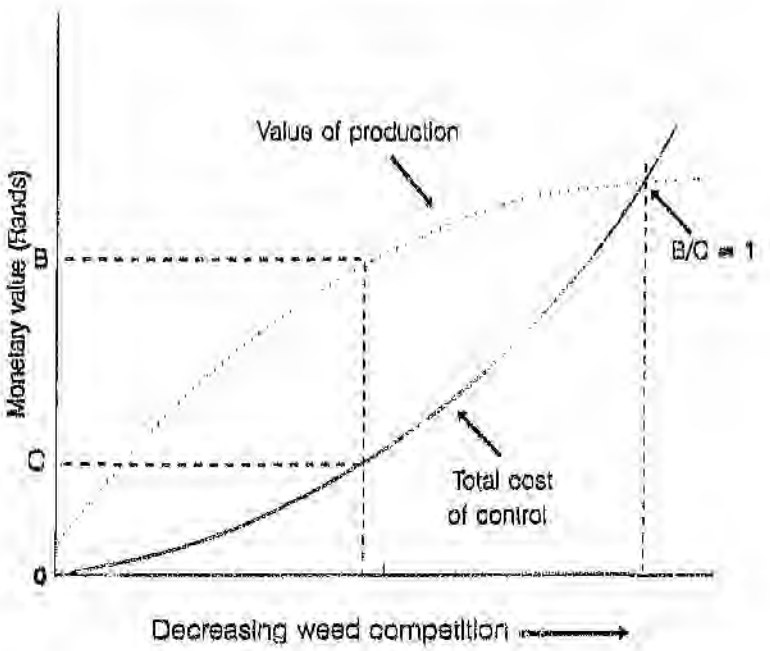

Figure 2.1. Hypothetical relationship between the value of production (B) and the cost of controlling competition (C) (Wagner *et al.* 1989).

2.2.2 Modelling competition

Models for inter-plant competition have been developed at different levels of complexity. In most studies of quantitative aspects of competition, regression models are used to describe competition effects empirically. Most of these regression models are static - they describe competition effects at a certain moment in time (Kropff 1988). Kimmins *et al.* (1990) refers to these as 'historical bioassay' models. The hyperbolic yield density equation for the description of timber yield loss in relation to weed density is an example of this category of regression models. In this type of model, a description is supplied of the yield at a given weed infestation at a given moment in the growing season. Willey and Heath (1969) carried out an extensive review of the quantitative relationships of plant populations and crop yield in which they examined the usefulness and biological validity of different mathematical equations. They concluded that, to describe these relationships realistically over a wide range of densities, and to construct yield density relationships, it was more desirable to use an equation with a biological foundation. In general, they found that the reciprocal equation best fulfilled these requirements.

Negative hyperbolic curves describing the relationship between maximum stem volume of *Pinus ponderosa* and shrub abundance are given by Wagner *et al.* (1989). Similar relationships have also been derived for *P. menziesii* and *P. taeda* growing with different levels of woody vegetation (Brand 1986, Wagner *et al.* 1989). Examples of the use of this approach in agriculture are given by Kropff (1988) and Streibig *et al.* (1989). The hyperbolic yield-density equation fits well with data of additive experiments where only the weed density is varied. However, model parameters may vary strongly among experiments, due to the effect of other factors on the competition processes. One of the most important factors causing this variation is the date of weed emergence relative to the crop (Kropff 1988). To account for this, an additional variable may be introduced into the hyperbolic yield-density equation. Kropff (1988) suggested that it would be more appropriate to characterize the weed infestation in terms of the estimated leaf area of the weeds relative to the leaf area of the crop, early in the growing season. Besides these static regression models for assessment of yield loss at a given infestation, a few regression models with a dynamic character have been developed. These describe the time-course of competition with a set of logistic equations or extended hyperbolic equations (Kropff 1988).

The concept of threshold values is based on the use of these descriptive regression models. This concept was first applied by entomologists to improve insect pest management decisions (Metcalf and Luckmann 1982). Much of the terminology used in insect pest management can be applied to plantation weed management. For example, the "economic injury level" would define (the weed density at which the value of the timber loss equals the cost of the treatment) and the "economic threshold limit" (the weed density at which control measures should be taken to prevent an increasing weed population from reaching an economic injury-level). These are fundamental principles of integrated pest management

The advantages of a Nelder experiment are that only a small area is required to examine the effect of an array of densities. Disadvantages are the difficulty of placement, and that only individual plants can be measured. Consequently it is difficult to obtain the effect of neighbouring tree associations. A further disadvantage is the difficulty in analysing Nelder designs statistically.

Addition series experiments are another systematic method for describing plant interactions. Here a multiple species reciprocal yield equation is used to determine the yield of a species, based on the total and relative densities of all the other species in a tree-weed mixture (Radosevich 1987). Data are analyzed from an array of species densities and proportions. For example, in assessing the competitive effect of a grass species on a tree species, the experimental design may form a simple matrix of the two species with variations in species proportions and densities per plot. This approach could be valuable for studies of tree and weed interactions since the effects of inter- and intraspecific competition can be separated through systematic variation of total density and species proportions. Shainsky (19[illegible]ed addition series experiment to examine the mechanisms of competition between *P. menziesii* and *A. rubra* (Shainsky and Radosevich 1992). As with substitutive experiments, additive series experiments are not fully applicable to plantation forestry where the density of trees remain constant.

2.2.1.4 Neighbourhood experiments

Neighbourhood experiments may be appropriate to assess interference when individual responses to the proximity or zone of influence of other plants is of primary interest. However, defining a zone of influence for use in a competition index for individual trees that includes all competitors and sources of competition for scarce resources is difficult. Generally, researchers have determined empirically that larger influence zones provide better correlations with growth (Biging and Dobertin 1992). In neighbourhood designs, the "performance" of a target individual is recorded as a function of the number, biomass, cover, aggregation or distance of its neighbours (Radosevich 1987, MacDonald 1991). For example, in this study, the target individual would be *P. patula*, and the trees performance would be recorded in relation to *S. megaphylla*. Generally, four types of neighbourhood models have been used based on the quantification of:

- competition around an individual tree as a result of crown overlap with neighbouring trees,
- number of surrounding neighbours (local crowding),
- area available, and
- composite statistics accounting for size, distance and spatial arrangement (Wagner and Radosevich 1991).

fixed espacements, it is assumed that spatial arrangements among trees in additive experiments are uniform and that the influence of intraspecific competition is therefore constant. This is not true if trees in one treatment grow bigger than trees in another treatment, nor is it the case with weeds, where placement is usually irregular and often unknown. Because of the uncertainty of proximity factors and the inability to differentiate between intra- and interspecific effects, determination of the causes of competition are difficult.

2.2.1.2 Substitutive experiments

The *substitutive* approach to studying competition could overcome much of the criticism of additive experiments (Harper 1961). In a substitutive experiment, the total plant density remains constant, while the mixture proportions of the two species vary (Shainsky and Radosevich 1986). The premise of substitutive experiments is to determine the yields of mixtures by comparing them to monoculture yields. Therefore, in this study the proportion of *P. patula* would be varied in relation to that of *S. megaphylla*. The two experimental variables, density and proportion are not confounded as density is held constant.

Substitutive experiments are useful for assessing the competitive effects of species proportion at a single total density (Radosevich 1987). It is also possible to determine the relative effects of intra- and interspecific competition using this design. However, partitioning of the absolute effects cannot be accomplished. Substitutive experiments are not a true reflection of plantation forestry, where constant rather than variable tree densities are used. The method is also cumbersome when studying mixtures of species of different life strategies or growth forms.

2.2.1.3 Systematic methods

Systematic methods include Nelder experiments and addition series experiments (Radosevich 1987). Traditionally Nelder experiments have been restricted to the study of interference among individuals of a single species where the plant density and spatial arrangement are varied systematically (Cole and Newton 1987). For example, a Nelder design was used to evaluate the effects of tree density on the distribution of tree and pasture grass roots (Eastham and Rose 1990). Nelder designs consist of a grid of plants, usually planted in an arc or circle. The area per plant, or the amount of space available to each plant, changes in a consistent manner over the grid. By "overseeding", the influence of a competitor species can be introduced into the Nelder experiment. This implies that the effect of intraspecific competition under the constant influence of a "background" species could be determined.

identical, micro-environments. *Interspecific competition* involves adverse interference among plants of different species.

The objective with respect to vegetation management may be viewed as shortening the time between the initial and later stages of succession by providing conditions which favour the growth of the tree species until they can naturally outcompete competing vegetation.

2.2 Methods of competition study

2.2.1 Experimental designs

Most studies of conifer-weed interactions have assessed tree growth in response to a manipulation of weed populations with mechanical or chemical tools. Such studies are instructive and may meet the immediate needs of forest managers. However, they do not adequately quantify the relationship between conifer growth and weed density, or elucidate the underlying mechanisms of competition. Although the growth effects of competition are easily measured for example, height, diameter, volume and biomass, the causal factors are far more difficult to determine. Factors such as moisture, nutrients, light and growing space are so interrelated that it is difficult to pinpoint that factor which is most limiting to plant growth. The use of systematic designs may quantify conifer-weed interactions more definitely. Competition experiments can follow four basic designs, namely: additive, substitutive, systematic and neighbourhood experiments (Radosevich 1987). These are discussed below.

2.2.1.1 Additive experiments

In *additive experiments*, two or more plants species are grown together. Most studies are conducted with only two species. The density of the one species is maintained at a constant level, while the density of the other species is varied. This approach is perhaps the most common approach to studying weed competition. It is relevant to many forestry situations either in which at least one species of weed infests an area already occupied by a fixed density of trees or in which varying densities occur as a result of different weed control treatments (Schoener 1983; Radosevich 1987).

The additive method has been criticized because it does not fully account for the influence of density and species proportion on the outcome of competition. Total plant density always varies, while the proportion among species also changes simultaneously with total plant density. With two factors varying at the same time, interpretation of the effects of either factor becomes difficult. As trees are planted in

- the density, depth and morphology of water and nutrient absorbing roots;
- the mode of reproduction (reproduction from seed favours migration into other communities, while vegetative reproduction is favourable to the maintenance and enlargement of an existing community); and
- the regenerative capacity (important after temporary suppression as a result of mechanical disturbance).

Most plants adapt more than o ie of the above strategies and often strategies overlap.

Specific factors responsible for the decrease or elimination of one of the competing species fall into two classes of mechanisms: direct (also called exploitative) or indirect (also called interference competition). In exploitative competition, individuals, by using resources, deprive others of benefits to be gained from these resources. Interference competition is when individuals harm each other, but not through pre-emptive resource use (Colliler *et al.* 1973).

Schoener (1983) identified four basic mechanisms of competition in plants:

- *Consumptive* competition occurs when some quantity of resource e.g., water or nutrients is consumed by an individual, thereby depriving other individuals of it (exploitative).
- *Pre-emptive* competition occurs when a unit of space is passively occupied by an individual, thereby causing other individuals not to occupy that space (exploitative/interference). In many natural plant populations, a size distribution arises in which most plants are suppressed and small, but a few are large and dominant. The place that an individual occupies within this hierarchy of size classes is apparently determined at a very early stage of development.
- *Overgrowth* competition occurs when another individual or individuals grow over or upon a given individual thereby depriving that individual of light and possibly harming that individual as a result of physical contact (interference or exploitative). This type of competition could be both positive or negative. Radosevich and Osteryoung (1987) cite a number of examples of increased survival of conifer seedlings under shade. The possible mechanism is a moderation of environmental factors such as moisture, temperature or light.
- *Chemical* competition or allelopathy occurs when an individual produces some chemical (toxin) which diffuses into the medium or substrate and harms other individuals (interference).

Competition may also be defined in terms of interactions within and between species. *Intraspecific competition* is the negative interaction between plants of the same species. The interaction between trees in even-aged plantation forestry is an example of intraspecific competition. Intraspecific competition is usually very intense because closely related individuals must exist in similar if not

Resources are any materials or factors which are consumed by a plant and which will consequently lead to increased growth rates and yields. Resources include light (the energy for photosynthesis), gases (for photosynthesis and respiration) water and nutrients.

The resources available to the trees and the physical conditions that the tree is exposed to make up the environment or site. Plant species distribution has been related to a number of environmental factors, and their ability to tolerate these factors. This is known as the *theory of tolerances*. Radosevich and Osteryoung (1987) summarize the main elements of this theory as

- The succesful existence and reproduction of a plant species will be determined by a set range of environmental factors.
- Generally in order of importance, the environmental factors are climatic, edaphic and biotic.
- The tolerance range is species-specific and dynamic altering with the age, size, and phenological stage.
- The tolerance ranges are determined by the physiological and not morphological features of a plant species.
- The process of natural selection may change the tolerance range. This slow adaptation to a new set of environmental conditions will be accompanied by the faster process of plant migration to a similar tolerance range elswhere.
- Species with similar tolerance ranges will compete with each other for resources and in so doing determine their relative distribution within a range.

From a forestry perspective, the actual tolerance range and ability of the tree species to grow in the presence of other competing plants occupying the same tolerance level is important. Current evolutionary theory holds that selection pressure drives species within a community to utilize different parts of the environment, with the result that competition is minimized through niche separation.

Successful competitors have characteristics which maximize the acquisition of resources in productive but relatively undisturbed habitats. This can occur during the early stages of re-afforestation. The competitive ability of a species depends on its genetic potential which is manifested in its morphological structure and its physiological requirements (Meuller-Dombois and Ellenberg 1974). These include:

- the germination and growth rate;
- the development or life history of a species (where species with the same life history are strong competitors while species with different life histories are complementary);
- the final height of the species;
- the longevity of the species;

2. LITERATURE REVIEW

The literature review concentrates on interspecific competition within plantation forestry, with particular emphasis on the genus *Pinus*. It commences with a broad overview of the ecological concepts of competition. Approaches to studying competition are evaluated and the concept of modelling competition discussed. Competition in terms of growth and survival, and the physiological basis of competition are also reviewed.

2.1 The ecological concepts of competition

Along with predation and mutualism, competition is one of the three major kinds of biotic interactions (Keddy 1989). The value of competition can be judged by its contribution to the development of ecological theory. Knowledge of the ecological principles that govern plant growth and the application of ecological concepts are important in developing management regimes.

There is a wealth of information, observations, experimentation, hypotheses, concepts, theories and models regarding competition. The objective should be to organize this information so that the output in some way appears consistent with observations, so that we can in some way begin to understand and predict the nature of competition.

There are a broad range of definitions of competition (Harper 1961, Odum 1971, Keddy 1989). Often the definition used relates to the management or study objective. From an agronomical or silvicultural point of view, the primary concern is to the degree to which a crop exploits an environment or site and how competing vegetation by negative effects restricts optimum usage of that resource and hence yield. Ecologically the emphasis would be on the processes and reasons for competition

For the purposes of this thesis competition is defined as:

> *Under a set of conditions, the negative effects which one plant species has upon another by consuming or controlling access to a limited resource.*

Conditions are factors that influence the survival and growth of plants but are not directly consumed by the plant. Examples are climatic factors such as temperature and wind, edaphic factors such as topography and slope, physical properties of the soil and biotic factors such as insects, pathogens and weed competition. Important climatic, edaphic and biotic factors are summarized by Radosevich and Osteryoung (1987).

S. megaphylla. *S. megaphylla* recorded the second highest score in a weed index rating of 234 species on Frankfort Plantation in Mpumalanga (Viljoen 1992). The vigorous growth of *S. megaphylla* enables it to colonize cleared areas and suppress newly planted trees. Although usually restricted to roadside verges in first rotation compartments, scarification and amelioration of the mineral soil during harvesting operations creates an ideal seedbed. This results in an influx of the grass into second and subsequent rotation compartments. The dense growth of the grass also limits accessibility and facilitates the building of runs by rodents which in turn inflict damage on the trees. Considerable numbers of caryopses are produced annually, providing *S. megaphylla* with a large propagule reserve and the potential of further infesting forest plantations (Erasmus and van Staden 1983).

Currently *S. megaphylla* is controlled using either mechanical or chemical treatments (Kvitzau and Darrow 1983). A sound weed management strategy with respect to *S. megaphylla* requires an in-depth understanding of the processes involved in, and the consequent effects of weed competition on the growth of *P. patula*. No empirical studies have been carried out to determine the effect of *S. megaphylla* on the growth of *P. patula*. Neither have causal factors of com, been investigated. Therefore, no sound management practice based on the principles of cost benefit analyses, economic injury levels and competition threshold values can be instituted.

One of the principle objectives of the management of short rotation timber plantations is to obtain maximum merchantable yield in as short a time frame as possible. In order to accomplish this objective, the manner in which the trees interact with each other, with competing vegetation and respond to the environment they grow in should be understood.

The purpose of the two species competition trial was to determine:

- The degree to which *S. megaphylla* suppresses the growth of *P. patula*;
- The level of *S. megaphylla* infestation necessary for a suppressive effect on *P. patula* to occur;
- The duration of the suppressive effect of *S. megaphylla* on *P. patula*; and
- The reasons why *S. megaphylla* inhibits the growth of *P. patula*.

This dissertation comprises chapters reviewing relevant literature, the design and results of a competition trial in which *P. patula* was exposed to different levels of *S. megaphylla* competition and an investigation into the possible competition mechanisms.

- restricting the amount of photosynthetic tissue produced;
- by modifying the ability of stomata to respond to changing environmental conditions;
- by increasing respiration as resources are shifted from one metabolic process to another (Waring and Schlesinger 1985); or
- by reducing the quantity of the carbon assimilation enzyme, ribulose bis-phosphate carboxylase (Long and Hällgren 1993).

Nutrient uptake by plants may remove an appreciable proportion of the whole ecosystem supply of available nutrients from circulation. In some types of ecosystems, though the actual uptake may be quantitatively small, it can represent a large proportion of the available nutrients. Under these circumstances, large woody plants which, as a consequence of their large standing biomass, require a greater amount of nutrients to complete their life cycle, may not be able to compete with smaller shrubs or herbaceous plants. In general, plants which produce more dry weight and leaf area for a given nutrient uptake are better suited to compete when a particular nutrient is limiting (Etherington 1975). The success of a plant in gaining a greater share of a limiting nutrient may cause such an increase in growth that a competing species may be suppressed secondarily by competition for light or water.

The competitive exploitation of soil nutrients may also be influenced by the rate of nutrient absorption by the rooting system of a plant. Endo- and ecto-mycorrhizae colonizing the root system can significantly improve the nutrient-absorbing characteristics of a plant (Waring and Schlesinger 1985). The spectrum of mycorrhizae colonizing roots may vary according to the nature and species of the root. Competition for rhizosphere space can occur if root systems are sufficiently extensive. Plants also show considerable variation of rooting depth within the soil profile, and are capable of removing and translocating nutrients to impose long-term and persistent patterns which create nutritionally differing microniches within the soil fabric (Etherington 1975).

In Ontario, Canada, Sutton (1975) found that controlling grass competition with the herbicide paraquat increased foliar nitrogen, phosphorous and potassium by 2.6, 1.5 and 3.1 times respectively for *Picea glauca* on a poor site. These advantages continued for three years. Releasing *P. ponderosa* from woody shrub competition on two sites in California improved soil and foliar nitrogen levels for up to five years after treatment (Powers 1983).

Competition for soil nutrients was examined in five year old plantations of *P. menziesii* growing alone or with either of two competitors, grass (*Elymus* spp. and *Agrostis tenuis*) or red alder (*Alnus rubra*), on three different site types in the Oregon Coastal Range. *P. menziesii* foliar nitrogen concentration and total and available soil nitrogen did not differ significantly with competitor species. However, foliar

The three treatments were:

- low competition (near complete control for two growing seasons);
- medium competition (single broadcast application of a herbicide at the beginning of the first growing season only); and
- high competition (no herbaceous vegetation).

Soil moisture was found to be negatively correlated with the density of herbaceous vegetation. The effects of herbaceous weed levels on pine growth were attributed in part to differences in soil moisture, and their effects on seedling water status and physiological processes.

In a competition experiment in California, *P. ponderosa* seedlings were planted in hand-thinned plots of manzanita (*Arctostaphylos patula*) seedlings in a modified replacement series with five tree to shrub proportions approximating 0:100, 25:75, 50:50; 75:25 and 100:0 (Shainsky and Radosevich 1986). The depletion of soil moisture was greater in mixed stands than in the pine monoculture. Leaf water potential of trees was less negative and leaf conductance was significantly greater in the monoculture than in the mixed stands. Leaf conductance of *A. patula* seedlings was consistently higher than that of pine seedlings. These results suggest that competition with *A. patula* for soil moisture can reduce *P. ponderosa* productivity significantly during early site development.

Woods *et al.* (1992) evaluated the importance of competition between trees and weeds for water and nitrogen in a *P. radiata* plantation between two and three years of age in South Australia. The weed control treatments were 1, 2 and 3 m wide cleared strips spanning the tree row. Differences in predawn needle-water potential were small and generally not statistically significant. Smethurst and Nambiar (1989) reported that if weeds were removed in a 1 m wide strip spanning the tree row, predawn needle-water potentials remained greater than 0.9 MPa, and were not significantly affected by wider weed control strips. These results suggest that weed control in a 1 m wide strip was sufficient to alleviate water stress in trees during the initial two to three years after planting.

2.4.3 Competition for nutrients

Competition for nutrients may result in a reduction in the nutritional status of the plant, with a consequent decrease in the rate of the biochemical processes. Deficiencies of a critical nutrient may reduce carbon assimilation by:

increased available water as needle water potentials were lower and stomatal resistance much higher in the presence of weeds during dry conditions. Eckart (1979), working with *Pinus jeffreyi* and *P. ponderosa* showed depletion of soil moisture by perennial grasses. Control of the grasses with atrazine resulted in increased soil moisture and decreased soil moisture tensions during the growing season for two years following treatment. In an eight to twelve year old *Pinus pinaster* plantation, 16% of volume increment was lost through competition, which was principally for soil moisture (Butcher 1980).

Nambiar and Zed (1980) examined the effects of weed control on the needle water potential of *P. radiata*, on sites with high, medium and low weed control. They concluded that on sites that are relatively dry, even 5 - 10 % surface weed cover could induce water stress high enough (-1.5 to -1.8 MPa) to impair growth of young *P. radiata*. Sands and Nambiar (1983) investigated the water relations of *P. radiata* in competition with weeds. Soil water profiles, needle water potential and stomatal resistance were measured in *P. radiata* plantations growing with and without competition. In weed infested areas, severe water stress with consequent productivity loss occurred. The severity of stress decreased progressively with increasing tree age. Trees not subjected to weed competition were not water stressed over this period, even when planted at three times the normal stocking rate.

In a five year trial to determine the effects of site preparation with three levels of shrub suppression on the growth of *P. ponderosa*, *P. lambertiana* and *A. concolor* in northern California, predawn and midday water potentials were greatest when shrub control was most complete (Lanini and Radosevich 1986). Competition for moisture in five year old *Pseudotsuga menziesii*, alone or with either of the grasses *Elymus* sp. and *Agrostis tenuis* or red alder (*A. rubra*), was examined on three different sites in the Oregon Coast Range (Cole and Newton 1986). Predawn moisture stress varied with site, competitor and density. The lowest stresses occurred at low densities where *P. menziesii* was growing alone. For each treatment, moisture stress was found to be highest at high stand densities. This reflected the increased demand and faster depletion rate found at those density levels. The grasses were shown to compete with *P. menziesii* seedlings primarily for moisture. The *A. rubra* moisture stress values suggest that they were tapping water at deeper levels than *P. menziesii*.

In east-central Alabama, herbicides were used to create three herbaceous vegetation treatments in a two year old *P. taeda* plantation (Zutter *et al.* 1986b). The treatments were based on the duration and degree of herbaceous vegetation control during the first two growing seasons following planting.

to control transpiration and avoid excessive dehydration when water-stressed also result in reductions in CO_2 assimilation. These reductions are not necessary linear.

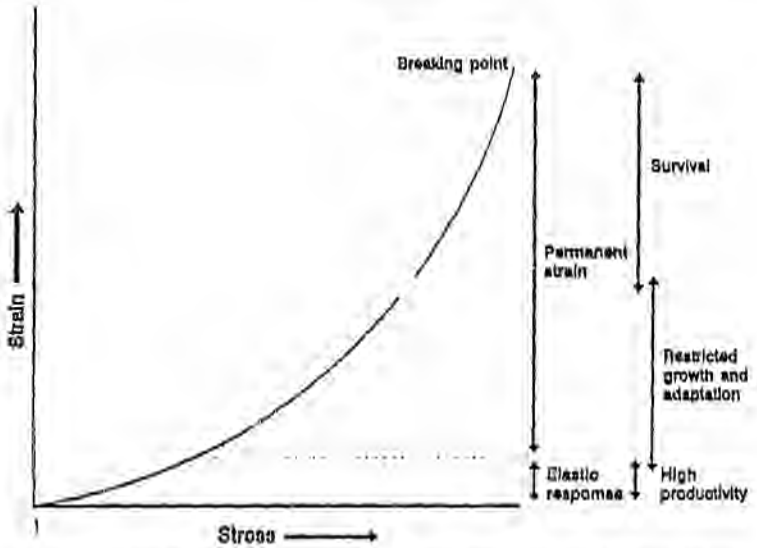

Figure 2.3. A generalized stress-strain diagram illustrating plant response to water stress modified from Bradford and Hsaio (1982).

As an adaptive strategy, the proportions of C allocated to various biomass components might change under conditions of water stress. Greater vegetative growth is characteristic of plants well supplied with water, when other factors are not limiting (Bradford and Hsaio 1982). The restriction in foliage growth as a result of water shortages is attributable to the high sensitivity of expansive growth to water stress. Increased competition for soil water or nutrients is likely to cause an increase in the allocation of carbon to fine root production at the expense of aboveground growth. Root growth under water stress also tends to confine itself to the relatively moist soil (Bradford and Hsaio 1982).

Soil moisture is often a critical factor for the establishment of tree seedlings on marginal sites (Havrenek and Benecke 1978). In South Africa it is an important component of site evaluation and classification for species selection. Plants which produce more dry weight and leaf area for the same water use are usually better competitors (Etherington 1975).

Ross and Walstad (1986) cite a study by Heidemann (1986) in which soil moisture content was compared between undisturbed, hoed, and chemically treated plots in a dense perennial grass community within a *P. ponderosa* stand. The chemically treated plots had the highest soil moisture throughout the dry months for two years following application. Hoeing increased the soil moisture content, compared to the undisturbed plots, but not as much as did the chemical treatment. Lambert *et al.* (1972), in studying the growth response of *Pinus resinosa* to weed removal, attributed growth to

are dynamic, and should be appraised on a number of time scales (Passioura 1982). Water stress in trees develops in the short term (hourly) as the rate of water uptake from the soil is slower than the rate of loss by transpiration. In the longer term, losses by transpiration and evaporation will reduce the amount and availability of soil water, which will ultimately have an effect on productivity. The relationship between transpiration and assimilation on a unit area basis (normally a leaf) is usually evaluated on daily or even shorter time scales. Photosynthetic productivity is usually considered over longer periods or growing seasons with respect to the net rate of assimilation of the whole plant, water supply, water use, and the efficiency of water use.

Water deficiency as a result of competing vegetation influences the physiology, morphology, and metabolism of the crop plant. Research on the plant response to water stress has usually been concerned with short term physiological responses such as plant water potential and stomatal control. Far less emphasis has been placed upon the longer term morphological responses (Passioura 1982). These short term effects may have only a small influence on the growth of a plant, although recently, quantitative data showed that very mild water stress is sufficient to have substantial effects on canopy size if the stress lasts for some time (Bradford and Hsaio 1982). In order to investigate the relationship between water status and plantation yield, a method is needed to integrate the effects of plant water status over time (Landsberg 1986). Photosynthesis and transpiration also depend on the leaf area and other morphological properties of the shoot. These in turn depend on past water status of the plant. Leaf area and morphology are often the most powerful means of influencing the water use productivity of plants (Bradford and Hsaio 1982). Myers (1988) investigated using a water stress integral to ascertain whether a relationship existed between short-term stress and long-term growth of *P. radiata*. Other physiological processes affected by water stress include respiration, accumulation and transport of specific metabolites and nutrient uptake.

Bradford and Hsaio (1982) describe plant responses to water stress in terms of a stress-strain interaction. The numerous physiological responses of plants to water deficits generally vary with the severity as well as the duration of the stress. As stress increases, these changes intensify, become less elastic and less reversible in their response, and additional processes become affected in accordance with their relative sensitivities to the stress. Figure 2.3 illustrates the generalized time course and adaptive changes of crop plants in relation to an intensification in water stress. The diagram emphasizes that several important adaptive changes occur well ahead of stomatal closure.

Generally, until a threshold ψ value is reached, assimilation is not sensitive to reductions in leaf ψ. When the leaf ψ decreases to below the threshold ψ value, CO_2 assimilation declines at an ever increasing rate. This can be to the extent of achieving a negative net photosynthesis rate due to respiration. The threshold varies widely for different species and environmental conditions. The means evolved by plants

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year study, while 38 % of shaded seedlings died (Strothmann 1967).

Cole and Newton (1986) worked on light relations in a five year old *P. menziesii* plantation under variable competition from *Alnus rubra* and the grasses *Elymus* spp. and *Agrostis tenuis*. They found that light measurements showed important differences in interception with canopy position and competitor type. Light interception by *P. menziesii* was lowest under the red alder (*Alnus rubra*) canopy. The grasses *Elymus* spp. and *Agrostis tenuis* did not compete significantly for light once the canopy of *P. menziesii* had closed. A number of competition indices use estimated light interception to determine the level of competition on tree growth (Brand 1986, de Long 1991).

2.4.2 Competition for water

Water is essential to all living cells. Any reduction in its availability due to competition might be expected to affect the vigour and ultimately the productivity of the plant. The assimilation of CO_2 during photosynthesis results in the loss of water through transpiration. The rate of transpiration depends on atmospheric conditions, and various morphological and physiological properties of the plant. Atmospheric conditions include light, temperature, humidity, and wind speed. Properties of the plant include the area and orientation of the leaves, and the stomatal and cuticular conductance to water vapour. The stomatal conductance depends on the water status of the plant, which in turn depends on the water status of the soil, the hydraulic resistances experienced in the transpiration stream, the transpiration rate, and the osmotic pressure of the symplast. The movement of water through the soil-plant-air continuum is along water potential gradients, and is driven through changes in leaf water potential as a result of transpiration. This water movement is analogous to the electrical resistance or Ohms law, and is discussed in detail by Passioura (1982).

In plantation forestry, competing vegetation is usually more predominant in the early stages of the establishment of a stand of trees. During this time, weeds may seriously affect the water balance of the site, and as a result, reduce the growth of trees. A close correlation has been demonstrated between forest productivity and available soil moisture, determined indirectly from precipitation and evapo-transpiration budgets (Kramer and Kozlowski 1960). The effect of weeds within the soil plant air continuum can best be evaluated by determining stand water balances. The determination of stand transpiration is vital for estimating stand water balances, water movement and availability through the soil profile, the rate of water movement through trees and competing vegetation, and the efficiency in which water is used under different levels of competition (Landsberg 1986).

Physiological and environmental processes affecting photosynthetic productivity in relation to water use

The rates of light saturated photosynthesis by leaves of C_4 plants is often greater than C_3 plants, as they are more efficient in their use of intercepted light energy (Landsberg 1986). Jones (1983) lists anatomical, biochemical, physiological and ecological characteristics of C_3 and C_4 plants. *S. megaphylla*, a C4 grass, has a photosynthetic rate of 10.98 μmol CO_2 m^{-2} s^{-1}.

Dry matter production depends not only on the rate of photosynthesis per unit of leaf area, but also on total leaf area, leaf dynamics (e.g. leaf initiation, senescence and shedding) and canopy exposure (Etherington 1975, Kramer 1986). Canopy structure plays an important role in the light interception process by influencing photosynthetic active radiation (PAR) extinction and duration of absorption. Growth patterns and the biomass allocation can be affected by the light regime. The amount of wood produced depends on how much photosynthate is used in respiration and how much is partitioned among the various organs of the tree. High PAR levels can result in increased root/shoot ratio of conifers, increased root and shoot (total) dry weight, increased apical growth, and root elongation (Radosevich and Osteryoung 1987).

The amount of incoming solar radiation intercepted by a forest canopy, together with its efficiency of conversion into dry matter, significantly affect levels of actual production on a specific site. High levels of production ar achieved through rapid leaf area development, which results in earlier occupation of a site and increased absorption of photosynthetically active radiation.

Evidence from agricultural literature ' that the growth rate of a crop is proportional to the radiation intercepted by its canopy (Monteith 1977). This linear relationship has been extended successfully to plantation species (Cannel *et al.* 1987, Cannell *et al* 1988, Landsberg and Wright 1989, Dalla-Tea and Jokela 1991, Raison and Myers 1992). The slope, ϵ, represents an estimate of light-use efficiency. A detailed description of the physiological basis of light-use efficiency and its use to analyse forest production is discussed by Landsberg *et al.* (1995).

As an example of its use, the canopy dynamics, light interception and productivity of six year old *P. taeda* and *P. elliottii* were investigated under different competition regimes (Dalla-Tea and Jokela 1991). Significant differences in aboveground biomass production were observed between the different competition regimes. The biomass production of *P. taeda* increased from 3.1 to 16 Mg ha^{-1} yr^{-1} and *P. elliottii* from 3.5 to 8.0 Mg ha^{-1} yr^{-1}. Differences were principally ascribed to greater leaf area indices and higher light use efficiency.

Pinus resinosa seedlings planted under dense shrub strata (*Corylus* spp.) were studied to evaluate the effect of two light levels on growth. No severe drought was encountered during this period. Elimination of competition improved all aspects of seedling growth. No unshaded seedlings died during the two

compared a simple radiation model, where needles were randomly located and distributed symmetrically, and a non-random (grouping) model, which used measurements of canopy structure as inputs. They found that the grouping model was more accurate, which emphasizes the importance of branches and stems with respect to shading. Needles at the top of the canopy, and those not exposed to shading by competing vegetation, are physiologically and anatomically conditioned by the high irradiances they experience. In contrast, needles situated lower down in the canopy or which are shaded by competing vegetation are more shade-adapted. The maximum rates of photosynthesis are larger in shoots which have developed at higher, exposed levels in the canopy. As the level of shading increases, the minimal stomatal and mesophyll resistances increase and the dark respiration rates and compensation irradiances decrease. Photosynthesis of shaded needles is not restricted by the radiation-saturated rate as irradiances are low. The photosynthesis of shaded needles is largely limited by the photochemical efficiency of these needles. Therefore, increases in chlorophyll or other pigments, and increases in the absorptivity in the shaded needles would be expected to lead to increases in photosynthesis (Jarvis *et al.* 1976).

A considerable range of light requirements exists amongst different types of plants. These requirements are based on modifications which maximize the net assimilation rate or relative growth rate for a given energy input during the life of a photosynthetic organ. These may be associated with:

- minimizing respiratory loss;
- maximizing photosynthetic rate for any level of energy output; and
- alteration of leaf area ratio (an increase will give a larger relative growth rate for the same net assimilation rate) (Etherington 1975).

The ability to maintain a positive carbon balance (i.e. photosynthesis exceeds respiration) at low irradiance levels varies with species. Species with high photosynthetic rates generally do not grow as well at low irradiance levels as those with lower rates. Photosynthetic efficiency at low light levels has also been correlated with the degree of shade tolerance. Generally, shade tolerant species exhibit lower levels of photosynthesis at light saturation and higher photosynthetic rates at very low light levels than do shade intolerant species.

The maximum potential for growth will be partly determined by the maximum photosynthetic capacity of a species. Photosynthetic rates range from 2.6 to 17.2 μmol CO_2 m^{-2} s^{-1} for conifers (Jarvis *et al.* 1976, Landsberg 1986). The maximum photosynthetic rate for *P. patula* is 7.5 μmol CO_2 m^{-2} s^{-1} (Christie *unpubl.*). In general, the leaves of deciduous trees and shrubs have the potential for higher photosynthetic rates than those of conifers (Waring and Schlesinger 1985).

2.4 Physiological basis of competition

As seen from the survey of literature in sub-section 2.2, most studies indicate that negative interactions occur when plantation tree species are exposed to competing vegetation.

The understanding and prediction of plantation growth as a result of competition is determined by the physiological responses to the resources and conditions that characterize the site or environment in which the trees grow. The physiological processes are the mechanisms through which the genetic potential of a species and environment interact. The genetic potential determines the nature and limitations of the physiological mechanisms, but actual productivity is determined by the environment in which the trees are growing.

The best understanding of the mechanisms underlying competition arises when limiting factors are identified, and the responses to these factors can be demonstrated (Landsberg *et al.* 1991). This sub-section discusses the principles relating to physiological process with respect to competition for light, water and nutrients.

2.4.1 Competition for light

Light provides the energy for photosynthesis and is a fundamental requirement for plant growth. Competition for light occurs when a plant casts shade upon another plant. This could be due to its larger size, more rapid rate of growth, or earlier occupation of the site.

Although the physics of light transmission are well understood (Swift 1976, Campell 1981, Jones 1983) and there are detailed mechanistic (e.g., Farquhar and von Caemmerer 1982) and empirical (e.g., Charles-Edwards 1982) models of photosynthesis, models of the interception of light in forest stands still require a suitable description of canopy structure. Descriptions of canopy structure require a knowledge of internal structures such as leaf orientation, crown shape and spatial patterns of trees (Oker-Blom *et al.*1991). Norman and Jarvis (1974) describe the structure of a *Picea sitchensis* canopy at three levels: the vertical distribution of needles, branches, and stem; the inclination and orientation of needles on shoots; and the grouping of shoots into branches. The effect of competing vegetation further compounds the description of canopy structure and the effect it has on light interception and photosynthesis.

The needles in different parts of the tree canopy are exposed to large differences in irradiance. This self shading is a result of the orientation and density of needles and branches. Norman and Jarvis (1975)

decreased specific leaf area.

In the south eastern USA, height and diameter growth of *Pinus palustris* seedlings were compared between plots receiving herbaceous weed control treatments and on unweeded check plots during the first four years after planting. Weed control had a positive effect on fourth-year height, root collar diameter, and the percentage of seedlings out of the 'grass' stage, while survival was unaffected (Nelson *et al.* 1986).

A study in Arizona compared the competitive influence of two grasses, Arizona fescue (*Festuca arizonica*) and mountain monthly (*Muhlenbergia montana*) on *Pinus ponderosa* seedlings (Ross and Walstad 1986). Seedlings were grown alone and in competition with each of the grasses. Root and shoot growth of pines was significantly greater in the absence of grass competition. Roots of both species grew 50% faster than pine roots. At the end of two years, the dry weight biomass of grass roots was 11 to 16 times that of tree roots. Lanini and Radosevich (1986) reported an increased height (20 to 90%) and stem diameter (55 to 165%) of *P. ponderosa*, *Pinus lambertiana* and *Abies concolor* when shrub competition was controlled. No differences in survival occurred between the various treatments. However, Wagner *et al.* (1989) reported that survival and growth of *P. ponderosa* decreased in a consistent manner as levels of interspecific competition increased. Further studies on increased growth and survival in *P. ponderosa* have been reviewed by Ross and Walsted (1986).

Britt *et al.* (1991) carried out classical growth analyses on six year old *P. taeda*. Trends in data suggested that the growth parameters, mean relative growth rate, mean net assimilation rate and mean leaf area were confounded with size. To remove the potential confounding effect of size, the basis of comparison was changed from trees of equal age to trees of equal biomass. For a given biomass, trees in the low weed abundance treatment had greater mean relative growth rates and mean leaf area ratio's than those in the high weed abundance treatment throughout the study period. As the biomass of the trees increased, the partitioning of carbon into leaf area appeared responsible for the increases in productivity associated with weed control.

The effects of intra- and interspecific competition on root and shoot biomass of five year old *P. menziesii* and *Alnus rubra* were studied in experimentally manipulated stands in the Oregon Coastal Range (Cole and Newton (1987). *P. menziesii* root biomass ranged from 7 to 420 g tree^{-1} and decreased dramatically with increasing *A. rubra* density. Increasing the *A. rubra* density also reduced the shoot biomass of *P. menziesii*. While increasing the density of each species reduced the root and shoot biomass per tree, proportional allocation of biomass to roots and shoots was not affected by competition.

In an establishment experiment in a bamboo forest in Kenya, emphasis was placed on the importance of keeping *P. patula* weed free in its early years. At three years of age, survival was nil in the untended controls. Slashing resulted in a survival of 20% and a mean height of 3.6 m, while clean cultivation resulted in a survival of 70% and a mean height of 4.9 m. In Angola, *P. patula* plantations were cultivated mechanically to eliminate weed competition (Wormald 1975). Alternatively, Donald (1971) considered weeding unnecessary for the establishment of *P. patula* on virgin, annual grassland sites in South Africa.

The effects of fertilization, cultivation and eliminating grass competition, on the growth of *Pinus radiata* during the first two years after planting were studied in Victoria, Australia. Grass competition was found to be the major factor restricting the growth of *P. radiata*. Squire (1977) concluded that grass competition could exert an over-riding influence on early growth of *P. radiata* by directly restricting growth, and by severely limiting the ability of trees to take advantage of favourable nutritional and physical properties of the soil. In a study carried out by Nambiar and Zed (1980) on the influence of weeds on the growth of young *P. radiata*, the length and weight of fascicles decreased markedly as the intensity of weed control decreased. In comparing the establishment requirements of *P. radiata* cuttings and seedlings in New Zealand, West (1984) found that removal of grass competition for a minimum of one year improved both height and diameter growth of both cuttings and seedlings at the age of five years.

Clarks and Haywood (1986) studied the growth of *Pinus taeda* on an intensely prepared site where a complete fertilizer application at planting, as well as the control of herbaceous and woody vegetation for the first four years, was carried out. This resulted in an increase in *P. taeda* volume at five years of age. As the fertilizer and competition control factors affected pine growth independently of each other, their effects were additive. Herbaceous plant control was the most effective treatment, increasing pine volume by 63%. Declining dry weights of herbaceous plant material indicated that pine was dominant at six years of age. Response to herbaceous plant control for this age was limited. Woody plant control did not significantly increase pine volume until the fifth year because the intensive site preparation retarded the development of the woody competition.

In a trial examining the effects of interfering vegetation on biomass, fascicle morphology and leaf area of *P. taeda* seedlings, those growing with no vegetation were consistently greater in diameter and biomass than those growing with vegetation (Zutter *et al.* 1986a, Zutter *et al.* 1986b). Seedling diameter and biomass were more responsive than height to a reduction in interfering vegetation. For a given seedling age, the proportion of biomass in branches increased as interfering vegetation decreased. Seedling age and the absence of interfering vegetation each increased the percentage of foliage biomass in four-needled fascicles, fascicle diameter, total length, sheath length, dry weight, and surface area, but

the samples. Roots were preserved in a 1% solution of phenol acetic acid (FAA). The *P. patula* and *S. megaphylla* roots were separated from each other and the *P. patula* roots were separated into coarse (> 1mm diameter) and fine (< 1mm diameter) categories. Root length was estimated by means of a modified line intersect method (Tennant 1975). As a 10 x 10 mm grid was used, the number of intercepts were multiplied by a conversion factor of 0.787 (Tennant 1975), to obtain root length in metres. Dry root mass was determined for the two species. Roots were dried at 65°C for two days. The roots were then ashed at 800°C for two hours to determine the ash correction factor. ANOVA was carried out to test for differences in *P. patula* root length and mass for the different competition regimes. Allometric equations, using d_2 as the independent variable, were used to derive root masses (w_{root}) for each measurement period and treatment.

In determining root distribution through the soil profile, four representative trees were selected in the destructive sampling zones of each treatment in replication one during 1989, and two representative trees per treatment in replication two and three during 1990 and 1991 respectively. Pits of 1.2 x 1.2 x 1.2 m were dug so as to expose the roots of a centrally positioned *P. patula* tree and adjacent *S. megaphylla* plants. In total, 24 profiles were sampled. A one metre square graticule with one hundred squares was placed against the face of the profile and a count by square was made of exposed *P. patula* and *S. megaphylla* roots. Vertical and horizontal frequency distributions were obtained at 100 mm intervals for *P. patula* and *S. megaphylla* under the six different competition regimes.

3.3.4 Competitive interaction between *P. patula* and *S. megaphylla*

The methodology to determine the competitive effects of *S. megaphylla* on the growth of *P. patula* has been discussed in the previous sections. The interaction between the two species was studied by examining the needle mass ($w_{1,leaf}$) and needle relative growth rate ($RGR_{1,leaf}$) of *P. patula* in conjunction with the leaf mass ($w_{2,leaf}$) and relative growth rates ($RGR_{2,leaf}$) of *S. megaphylla*. The interaction is shown schematically in Figure 3.5

Partitioning coefficients for roots (η_{roots}), stems (η_{stems}), branches ($\eta_{branches}$) and needles ($\eta_{needles}$) were also determined for the sample dates. In order to determine whether there were significant differences between η_{root}, η_{stem}, η_{branch} and η_{needle}, least square means (LSM) were computed for each possible interaction and all possible probability values for the hypotheses

$$H_0: \text{LSM of } \eta_{i,\,t,\,tmt} = \text{LSM } \eta_{i,\,t,\,tmt}$$

where i is a bio mass component for a specific date (t) and treatment (tmt) (SAS Institute Inc. 1987).

Aboveground biomass sampling of *P. patula* took place three times in the destructive sampling zone. A total of 82 trees were sampled. The sampling frequency, and sample number are presented in Table 3.5.

Table 3.5 The date and number of *P. patula* trees sampled for aboveground biomass.

Sampling date	Sample no.	Description
June 1989	34	• Replication 1 - 2 trees per treatment Replication 2-4 - 1 tree per treatment Perimeter of trial - 4 trees
July 1990	24	• Replication 2 - 2 trees per treatment
July 1991	24	• Replication 3 - 2 trees per treatment

After height and root collar diameter measurement, the trees were divided into needle, branch and stem biomass components. The oven-dried green biomass (w), in grams was then determined for each component.

3.3.3 The length, mass and distribution of *P. patula* and *S. megaphylla* roots.

The length, mass and distribution of *P. patula* and *S. megaphylla* roots were measured in the six treatments. Sampling was carried out during July 1989, 1990 and 1991. In studying root length and mass, one representative tree per treatment (for all four replications) was selected in the destructive sampling zone. A one metre square graticule with one hundred, 0.01 m^2 possible sampling points was positioned centrally over each pine tree. Eleven random core samples were taken in 1989 and ten in 1990 and 1991, with a 45 mm diameter, thin-walled soil core sampler (Foale 1980). Sampling depth was 600 mm. The soil core samples were kept in labelled plastic bags and sealed. The samples were washed with a hydropneumatic elutriator to separate roots and other organic matter from the soil (Smucker *et al.* 1982). All non-root matter, such as soil fauna, debris and dead roots were removed from

components under adverse conditions, where water, light or nutrients are limiting. The issue of the partitioning of assimilate between plant components is one of the biggest challenges in whole plant physiology research (McMurtrie and Landsberg 1992). Most models which calculate the productivity of forest stands from carbon uptake use constant biomass partitioning coefficients (a_i) -but these are unsatisfactory in a dynamic model.

Separate allometric equations were derived for each biomass component using root collar diameter as the independent variable. The allometric equation is

$$w_i = a_i d_c^{n_i} \tag{3}$$

or

$$\ln w_i = \ln a_i + n_i \ln d_c \tag{4}$$

where w_i is the biomass of the root, stem, branch or needle component.

The constant 'n_i' is often termed the 'allometric constant' (Hunt 1978), and is the slope in the logarithmic form. It provides a convenient and practical method of evaluating growth under different environmental conditions. Since n_i is the ratio of the logarithmic growth rates of d_c and w_i, any value other than unity implies that a discrepancy between the two rates will lead to a change in the relative proportions of d_c and w_i over time. By examining the variation in the constants (n_i) and the coefficients (a_i) between treatments and in time, one can deduce whether different patterns of dry matter allocation are occurring. In addition,

$$w_i = a_i W^{n_i} \tag{5}$$

where W is the aboveground or total mass of the tree, the mass of the various biomass components in relation to the total or aboveground mass at different ages can be determined.

Equation 4, in conjunction with the number of stems per hectare (S ha^{-1}), was used to determine the biomass for the different competition regimes for the duration of the trial. An ANOVA was also carried out to determine if there was any difference in biomass between the various treatments over the study period. Both the aboveground and total biomass were studied in order to develop an understanding of the relative importance of root biomass with respect to carbon allocation. The conversion of aboveground biomass from g tree^{-1} to Mg ha^{-1} enabled direct comparison with root biomass which was calculated as g m^{-2} and then converted to Mg ha^{-1}.

Relative growth rates

In order to examine the differences in growth of the various treatments over time, log transformations were carried out to express the exponential growth trends in a linear fashion. The variables were fitted to a $\log_e$-linear model of the form:

$$\ln Y = \ln a + b \ln X \qquad (1)$$

where Y is the height (m), d_c (cm) or volume index (m^3 ha^{-1}) and X is the time in days since establishment. This was carried out for every sample tree. To test for differences between treatments, the slopes (a) of the regression equations were then compared using ANOVA and Duncans multiple range test (SAS Institute Inc. 1987). This concept is similar to the mean relative growth rate (RGR) method used for comparing treatment differences on a uniform basis as described by Hunt (1978) and Britt (1991).

When comparing rates of growth over long intervals, such as annually or twice annually, it is likely that detailed growth and yield information will be subsumed. Therefore, RGR for root collar diameter (RGR_d), height (RGR_h) and volume index (RGR_v) were determined more frequently. RGR was defined as the growth of *P. patula* relative to the amount of growing material present or already produced for a certain time interval and expressed as:

$$RGR_X = \frac{\ln X_2 - \ln X_1}{t_2 - t_1} \qquad (2)$$

where RGR_x is the relative growth rate for a growth variable X for a time interval t.

3.3.2 The biomass of *P. patula*

Root collar diameter and especially height of seedlings are not always the best indicators of the competitive ability of a plant (Hatchell *et al.*, 1985). A plant's competitive potential is often manifested in differences in aboveground plant biomass and is an indication of photosynthetic area and the size of the root system. Biomass is often used to estimate competitive potential (Byrne and Wentworth 1988). Biomass is generally accepted as the most sensitive indicator of site preparation and other silvicultural treatment effects on tree growth, particularly for young trees (Haines and Davey 1979). While young trees may not exhibit increases in total height as a result of silvicultural treatments, they may have larger diameters, greater stem volumes, and more foliage (Haines and Davey 1979).

3.3 Growth and yield

The variables measured during the course of the trial are listed in Table 3.4.

Table 3.4. Variables measured in the trial (P represents *P. patula* and S represents *S. megaphylla*).

	Variable	Times measured	Interval between measurements
Growth	Height (P)	16 times	
	Root collar diam.(P)	16 times	
	Biomass (P)	3 times	
	Biomass (S)	continuous	
	Root length (P&S)	3 times	
	Root mass (P&S)	3 times	
	Root configuration (P&S)	3 times	
Moisture	Xylem pressure pot.(P&S)	13 times	
	Stomatal conductance (P&S)	10 times	
	Soil water	continuous	
	Soil water retention	once	
	Hydraulic conductivity	once	
Nutrients	Nitrogen (foliar & soil)	9 times	
	Phosphorous (foliar & soil)	9 times	
	Potassium (foliar & soil)	9 times	
	Magnesium (foliar & soil)	9 times	
	Calcium (foliar & soil)	9 times	
	N-mineralization	2 times	
Driving variables	Rainfall	continuous	
	Temperature (min. & max.)	continuous	
	Photosynthetic active radiation	continuous	

3.3.1 Absolute growth and relative growth rates of *P. patula*

Absolute growth

Height (h) and root collar diameter (d_0) for *P. patula* were measured sixteen times over the study period. Using these two variables, an estimate of aboveground wood volume (volume index) was obtained by multiplying the square of d_0 by h. This affords a better estimation of tree growth than either h or d_0 alone (Hatchell *et al.*, 1985). *P. patula* needle length was measured in order to determine whether competition affected their growth and development. In February 1989, 46 days after establishment, marker pins were inserted into branches adjacent to needle buds and needle length monitored. Three sets of needles per treatment were used.

With the exception of the control, which was kept weed free from the inception of the trial, *S. megaphylla* was planted in a geometric fashion between the *P. patula* trees at a fixed density of 6860 plants per hectare.

Figure 3.4 illustrates the positioning of *S. megaphylla* between the trees.

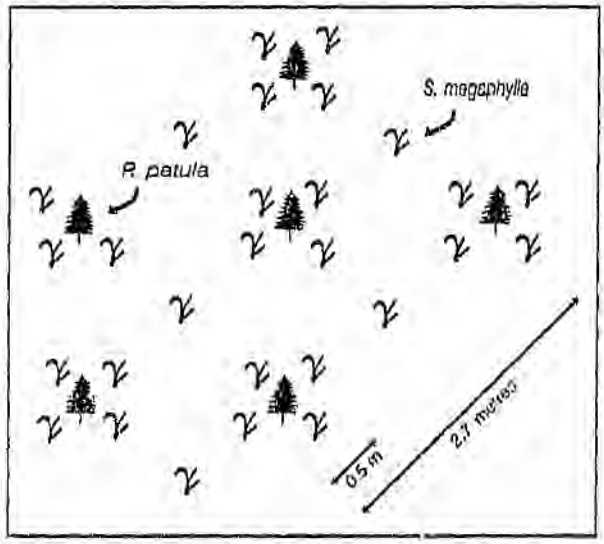


Figure 3.4. The positioning of *S. megaphylla* between the *P. patula* trees.

Five *S. megaphylla* competition regimes were instituted. This range of competition regimes was maintained by altering the frequency of clipping and consequently the aboveground biomass of the grass at any given time. Treatment A was clipped the most frequently and treatment D the least. Treatment E, the highest competition regime was left unclipped. The biomass of treatment E was determined by destructive sampling in the destructive sampling zone. The frequency, average biomass and leaf area index (LAI) removed during each clipping are illustrated in Table 3.3.

Table 3.3. The frequency of clippings and the average leaf biomass (kg ha^{-1}) of *S. megaphylla* removed from treatments during each clipping.

Treatment	Frequency	Biomass
Control	weed free	0
A	26	32
B	21	238
C	17	316
D	9	1160
E*	0	7471

* estimated from clippings in the destructive sampling zone.

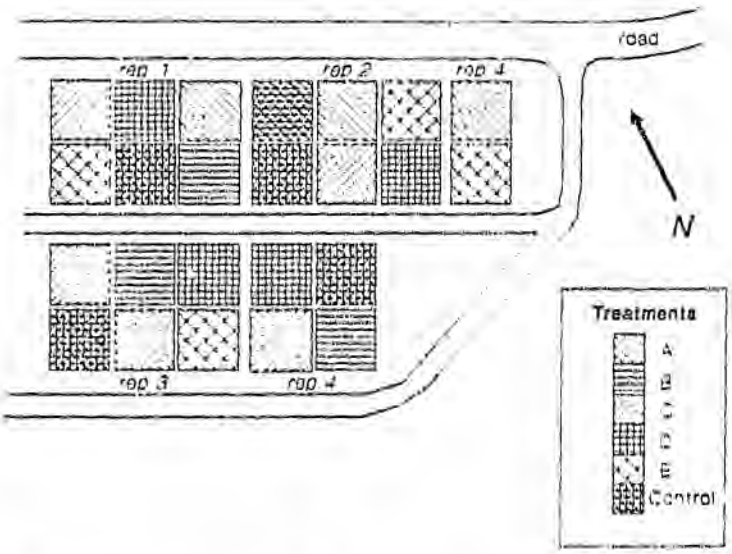


Figure 3.2. Schematic layout of the trial showing the position of the various treatments.

The trial was established in October 1988. Plots were square and 0.018 ha in area. Each plot had twenty-five *P. patula* trees planted at an espacement of 2.7 x 2.7 m. This espacement conforms to the standard prescription for *P. patula* planted under a sawtimber regime in South Africa (Wessels 1987). A buffer zone of one row of trees was included around each plot. To ensure that removal of trees had no effect on growth trends, destructive sampling took place in the two rows of trees immediately to the outside of the buffer zone (Figure 3.3).

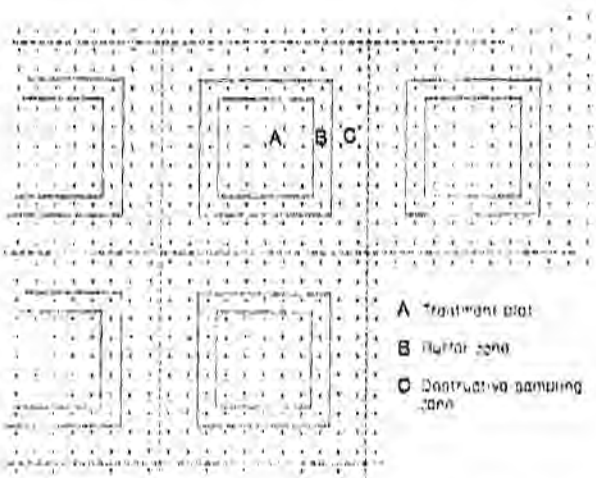


Figure 3.3. Detailed layout of the trial. Treatments were applied uniformly in the treatment plot and the buffer and destructive sampling zones.

The site, which was previously occupied by a *P. taeda* seed-orchard for approximately 20 years, was clear-felled, destumped using a rotary stump chipper, ripped and then rotovated to produce an even tilth. A month after site preparation, the site was sprayed with a 1% solution of glyphosate to kill any weeds present. The trial site was enclosed by a mesh fence to prevent trampling and browsing by livestock and game.

3.2 Design and treatments

The current trial is unusual in the sense that unlike most additive experiments, the densities of both *P. patula* and *S. megaphylla* were fixed and spatial arrangements constant. A competition gradient was derived by maintaining the leaf biomass of *S. megaphylla* at different levels. Landsberg (1986) states that a prerequisite for studying tree growth and physiology is the application of treatments that will cause large differences in the growth of trees, not to test whether the treatments cause differences.

The reason for this approach is that the biomass of *S. megaphylla* changes from a density-dependent to a density independent relationship over the growing season. At emergence, and while plants are small, the number of plants in an area (density) determines biomass. As plants grow larger, the point is reached when the supply of resources sets the limit to biomass produced. At this point, a further increase in density has little effect on yield. Conditions that slow the growth rate will tend to extend the time that yield is strictly related to density. In addition, proportions expressed as ratios of biomass may be more appropriate than ratios based on density when life forms of the species differ (Radosevich 1987). As the life forms of *P. patula* and *S. megaphylla* differ markedly, and the growth of *S. megaphylla* is so rapid that a density-independent situation is soon attained, it was therefore decided to maintain a constant density and manipulate the leaf biomass of *S. megaphylla*. This is also more appropriate in relation to the usual *S. megaphylla* control measure of slashing which reduces the leaf area rather than the density of the grass.

A systematic approach was decided upon in order to quantify the relationship between *P. patula* growth and *S. megaphylla* density and to attempt to explain the underlying mechanisms that might be involved in *P. patula / S. megaphylla* competition. In this study, the *S. megaphylla* population was manipulated by clipping to establish specific competition regimes so that the relationship between tree growth and grass leaf area could be examined. The clipping of *S. megaphylla* reflects the commonly employed weed management operation of slashing the grass. As the experimental units could be meaningfully grouped, a randomized complete block design was used. The object of grouping is to have units in a block as uniform as possible, so that observed differences will be largely due to treatments (Steel and Torrie 1960). Six treatments, replicated four times, were laid out in a randomized complete block design (Figure 3.2).

Table 3.1. Mean monthly rainfall (mm) and mean minimum and maximum temperatures (°C) for the period July 1959 to June 1989 (Anon. 1989).

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Rainfall	16.1	21.8	48.0	92.0	159.0	205.4	229.3	220.3	133.8	86.4		15.8
Min. Temp	6.9	8.8	11.3	13.0	14.6	15.9	16.7	16.7	15.7	13.1	9.9	6.9
Max. Temp	20.8	22.4	24.0	24.4	24.6	25.8	26.2	25.8	25.1	23.6	22.4	20.2
Mean Temp	13.8	15.6	17.6	18.7	19.6	20.8	21.5	21.3	20.4	18.3	16.1	13.5

The parent material of the soil is granite. The soils are ferrallitic, of the Farningham series of the Hutton form accord. g to the binomial classification system (Ma'. .car *et al.* 1977). FAO and USDA equivalents would b> rhodic ferrasols and ultisols (hapludalt) respec.vely. A summary of the chemical and physical properties of the soil are given in Table 3.2.

Table 3.2. Chemical and physical analysis of the A and B horizon.

Chemical	A Horizon	B Horizon
pH (H_2O)	4.5	4.9
pH (KCl)	4.1	4.9
Organic matter (g g^{-1})	0.0204	0.0101
Organic carbon (g g^{-1})	0.0118	0.0058
EA (m mol M* $100g^{-1}$)	0.66	0.58
extractable Al (mg kg^{-1})	59.4	5.4
N (mg kg^{-1})	1290.0	740.0
P (mg kg^{-1})	26.0	3.8
K (mg kg^{-1})	28.9	24.2
Ca (mg kg^{-1})	135.3	66.3
Mg (mg kg^{-1})	6.8	3.8
Physical		
Sand (%)		[1]
coarse	27	31
medium	16	8
fine	7	10
very fine	2	-
Silt (%)		
coarse	7	11
fine	18	-
Clay (%)	23	40
Bulk density (Mg m^{-3})	1.11	1.17
Saturated hydraulic conductivity (mm day^{-1})	1618	1557

[1] B Horizon sand, silt and clay percentages from Schulz (1989).

3. MATERIALS AND METHODS

3.1 Site description

The study site is located at an elevation of 950 m, on a north-east facing slope of 6° at the Frankfort Plantation near the town of Sable, in the province of Mpumalanga, South Africa (Figure 3.1). The precise co-ordinates are 25°3'10"S and 30°53'30"E.

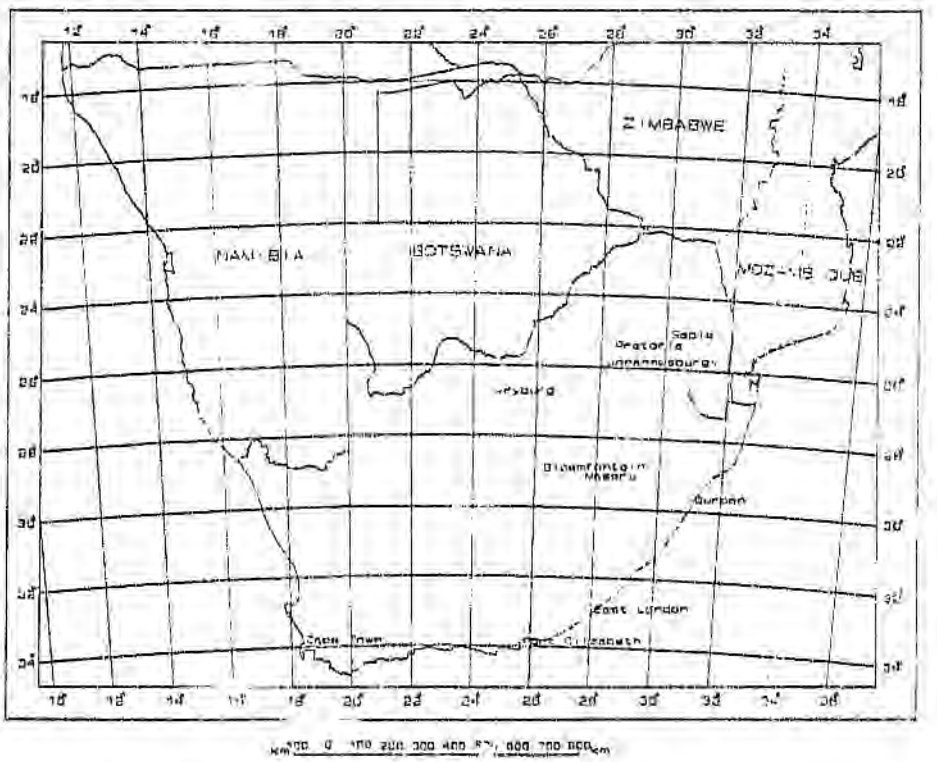


Figure 3.1. Map of South Africa indicating the position of Sable.

Over a 30 year period, from July 1959 until June 1989, the mean annual rainfall was approximately 1250 mm, with lowest rainfall occurring in June (15.8 mm) and the highest rainfall occurring in January (229 mm). The mean minimum and maximum temperature recorded for this period was 6.9 and 26.2 °C respectively. The climate is subtropical and frost seldom occurs. Mean monthly rainfall and mean minimum and maximum temperatures for the period July 1959 to June 1989 are given in Table 3.1.

Table 2.1. Foliar nutrient contents of *P. patula* (mg g^{-1}). Results from studies in Africa and South America. Adapted from Lundgren (1978), Grey *et al.* (1979), Morris (1986) and Schutz (1989).

Country	N	P	K	Ca	Mg
Brazil	17.9	1.3	6.1	2.7	1.0
Kenya	19.8	1.4	6.6	4.1	2.3
Madagascar	20.3	1.3	2.9	1.9	1.6
Kenya	-	-	9.3	2.8	1.7
Madagascar	16.7	1.3	7.3	5.3	1.7
South Africa	19.0	2.5	4.6	3.6	0.9
Swaziland	14.3-17.9	0.9-1.1	4.0-6.3	2.1-4.5	1.1-1.8
South Africa	21.5	1.8	8.7	2.6	1.7

Woods *et al.* (1992) studied the effects of annual weeds on nitrogen availability to young plantations of *P. radiata* in South Australia. They found that increasing the width of the weed control strip spanning the tree row increased the uptake of nitrogen by trees. Application of nitrogen fertilizer alleviated nitrogen deficiency and tree growth suppression induced by weeds, suggesting that when nitrogen supply is high, intense weed control is unnecessary in plantations beyond two years of age. However, in soils low in nitrogen, competition for nitrogen by weeds would seriously aggravate nitrogen deficiency in young *P. radiata* trees. When nitrogen fertilizer was applied, 68% was absorbed from the soil by the weeds compared to the unfertilized control. Weeds therefore increased the uptake of nitrogen fertilizer by plant biomass, and thereby improved nitrogen retention on the site. Tree growth increased with all levels of weed control and responses to weed control and nitrogen fertilizer were additive. The growth of weeds increased the soil organic carbon status and the rate of nitrogen mineralization.

Although photosynthetic rates of deciduous trees can be increased by up to five times with higher levels of nitrogen, conifers are less responsive to variation in leaf nitrogen content, with rates usually increasing by less than 25% upon fertilization (Waring and Schlesinger 1985).

phosphorus in *P. menziesii* was higher in the grass treatments. Both foliar nitrogen and phosphorus concentrations were significantly lower in trees planted at high densities (Cole and Newton 1986).

The effect of weed control on nutrient uptake of young *P. radiata* was studied in South Australia by Namblar and Zed (1980). The concentrations of foliar nitrogen, phosphorus and potassium in *P. radiata* were significantly reduced by weed competition, the adverse effect being more pronounced on nitrogen and potassium than on phosphorus.

Ellis *et al.* (1986), studied the effect of weed competition and nitrogen nutrition on the growth of *Eucalyptus delegatensis* seedlings in a highland area of Tasmania. Elimination of competing grass resulted in a faster growth rate, higher foliar N concentration and higher soil mineral N than in unweeded control plots.

Foliar nutrient data for *P. patula* are scant, and mostly collected from fertilizer trials and site studies rather than competition studies. In the Umzimkulu district of the Transkei, an attempt was made to relate foliar nutrient concentrations to the growth of *P. patula* (Grey *et al.* 1979; Payn 1985). However, results were disappointing - possibly as a result of the small sample size and the season of collection (spring). Foliar nutrient concentrations in *P. patula* are unstable in spring and sampling should always be undertaken in mid-winter (Payn *et al.* 1989). In Swaziland, Morris (1986) used foliar nutrient analyses in young trees to help interpret fertilizer responses. Samples collected from 11 sites indicated that only foliar phosphorus and potassium were correlated with volume increment. *Pinus patula* foliar nutrient levels in fertilizer experiments and nutrient cycling have also been variously reported from East Africa, Madagascar and Brazil (Lundgren 1978), but with few details given. Table 2.1 summarizes foliar nutrient concentrations for *P. patula* from these studies in Africa and South America.

ulic conductivity (K)) describes the conductivity of the soil to the flow of water and is determined by soil characteristics and the water content of the soil itself. The value of K increases exponentially with increasing water content, reaching a maximum, known as saturated hydraulic conductivity (K_{sat}), when the soil is saturated. The model predicts hydraulic conductivity from soil water retention curves and conductivity at saturation (van Genuchten 1980). Based on the Mualem theory, the soil water content (θ_l) as a function of pressure head (h) is given by:

$$\theta_l = \left(\frac{1}{1+(\alpha h_l)^n}\right)^m \quad (21)$$

where h_l are the pressure head values (cm) for *P. patula* and *S. megaphylla* either at field capacity (h_{fc}), wilting point (h_{wp}) or the critical level where stomatal closure occurs (h_{crit}). m is expressed as:

$$m = 1 - \frac{1}{B} \quad (22)$$

where α (l cm^{-1}) and β are estimated from observed soil water retention data.

The saturated water content of the soil horizon (θ_{sat}) is given as:

$$\theta_{sat} = \left(1 - \left(\frac{\rho_{soil}}{2.54}\right)\right) \quad (23)$$

where ρ_{soil} is the bulk density of the soil in the horizon. The bulk density of the soil will be affected by the percentage and density of stones[3] (2.54 g.cm^{-3}) in each horizon.

The air dry water content of the soil (θ_{ad}) is expressed as:

$$\theta_{ad} = \theta_m \cdot \rho_{soil} \quad (24$$

where θ_m is the gravimetric air dry soil water content (gg^{-1}).

Therefore, taking into account the saturated and air dry water content of the soil, the soil water content

[3] Assumed density of quartzite

the leaf area index has exceeded 2.5 (Hillel 1980).

The term s can be calculated from:

$$s = \frac{e_s\, 4098}{\sqrt{(237.3+T_m)}} \qquad (19)$$

where T_m is the mean temperature and (e_s) is given as:

$$e_s = 6.1078 \exp\left[\frac{(17.269 T_m)}{(T_m + 237.3)}\right] \qquad (20)$$

The equation uses daily temperature and net radiation as input variables. While Equation 24 is simple, its limitations are that α is supposed to incorporate the aerodynamic component of the Penman Monteith equation, and should be used for extensive uniform surfaces, where heights are uniform, there is zero surface resistance and a constant relationship exists between vapour pressure deficit and radiation (Hillel 1980 and Stewart 1983). Nevertheless, for the purpose of this comparative study, the use of Equation 24 to estimate potential evapotranspiration is adequate.

Soil water balance

In the water balance study, the supply of available water in the root zone of the profile is simulated from day to day as a running balance, with the soil profile compartmentalized into a number of layers. These layers account for vertical inhomogeneity of the soil and for the uneven distribution of moisture resulting from infiltration from the plantation floor into the top horizon only. Layers with similar hydrological characteristics are defined as belonging to the same horizon. Each of the soil horizons is characterized by a soil moisture retention and saturated hydraulic conductivity curve. Both are functions of pore size distribution.

For a given soil type, a unique relationship occurs between soil water content and soil water potential. This relationship is known as the soil water retention curve. This curve was determined for each horizon. The curve is derived by determining the energy status of water in the soil (MPa) at a series of water contents (Hillel 1980). The water potential of *P. patula* and *S. megaphylla* either at field capacity (ψ_{fc}), wilting point (ψ_{wp}) or at the critical level where stomatal closure occurs (ψ_{crit}), is derived from these curves.

A decrease in soil moisture content in the rooted zone results in a lower water potential in the soil, and restricts uptake by the roots. As transpiration continues, the plant loses water and bulk leaf water potential drops, resulting in stomatal closure. This causes a reduction of transpiration to the atmosphere but also limits the flux of CO_2 into the stomatal chamber and to the carboxylation sites in the leaf where photosynthesis takes place. In this way, a shortage of soil moisture may depress growth and yield.

The water balance of the study site can be written as

$$W = P - R - ET - D \qquad (17)$$

where W is the change in water content of the rooting zone, P is the net precipitation, R the net runoff, ET the total evaporation and D the deep drainage. P is the difference between gross precipitation and interception by the plant canopy. Interception loss can range from 5-60% and is function of canopy structure, storm size and rates of evaporation from the canopy surface (Landsberg 1986). Neither the amount of interception nor the stemflow was determined in this study. R is the difference between runoff and runon. The topographical position of the site precluded any runon. Units of all terms of the water balance equations are given in terms of equivalent depth units (mm). The water balance for all treatments was determined approximately two and a half years after establishment. The objective of the water balance study was to determine the relative differences in water balance outputs between the treatments rather than absolute values.

The parameter files used in the simulation of the water balance are presented in Appendix 12 and Appendix 13.

Evaporation

Evaporation from the soil and plant canopies of *P. patula* and *S. megaphylla* was estimated using the Priestley Taylor (1972) equation:

$$\lambda E = \alpha \left[\frac{s}{(s+\gamma)}\right](R_n - G) \qquad (18)$$

where E is the evaporation, λ is the latent heat of vaporisation of H_2O, γ is the psychrometric constant, s the rate of change (slope) of saturated vapour pressure with temperature, R_n net radiation, and G the soil heat storage or loss by conduction. In this model, G is not taken into consideration as it is assumed that an increase in heat storage early in the growing season will be compensated by a decrease at the end of the growing season. The value α is an empirical constant. From many sets of measurements this has been found to be close to 1.26 (Stewart 1983) although a value of 1.35 has been used when

Table 3.6. The date and frequency of ψ_{pine} and ψ_{grass} measurements.

Date	Age (days)	Intervals
06/12/1988	49	49
12/01/1989	86	37
21/02/1989	126	40
29/03/1989	162	36
16/05/1989	210	48
18/07/1989	273	63
19/09/1989	336	63

The relationships between $S\psi$, d_s and biomass for *P. patula*, and between $S\psi$ and cumulative biomass for *S. megaphylla* were investigated. Treatment E was excluded from this study due to insufficient biomass production data.

In addition to investigating the relationship between $S\psi$ and measures of productivity for *P. patula* and *S. megaphylla*, the interaction between $S\psi$ and cumulative soil water deficits-time for the A and B horizons were also studied. Cumulative soil water deficit-time ($\theta_{def\text{-}time}$) is defined as

$$\theta_{def\text{-}time} = \sum_{i=1}^{i=n} (\theta_{fc} - \theta_s)n \qquad (16)$$

where θ_{fc} is the volumetric soil water content at field capacity for the A or B horizon and θ_s the volumetric soil water content over an interval of n days.

3.5.4 The water balance of the different treatments

Introduction

Water movement in a vegetation canopy is determined by both physical and physiological factors. Physical site factors such as precipitation and the water-holding capacity of the soil regulate the water supply, solar radiation provides the energy for the evaporation process, and atmospheric conditions, together with the canopy roughness, determine the 'drying power' of the air. The canopy influences net precipitation input into the soil compartment by interception and redistribution of rainfall. When the canopy is completely closed so that direct evaporation from the soil can be ignored, the vegetation also controls the rate of water loss from the soil to the atmosphere by means of regulation of the transpiration flux. The combination of precipitation, evaporation of intercepted precipitation, transpiration, and direct soil evaporation, determines the rate of soil water depletion or replenishment and thus the flow of water through the system.

Stomatal conductances

Diurnal stomatal conductances for *P. patula* ($g_{s,pine}$) and *S. megaphylla* ($g_{s,grass}$) were measured using a null-balance porometer (Type 1600, LI-cor Inc., Lincoln, NE., USA). Stomatal conductance was expressed in molar units of moles m^{-2} s^{-1} (Jones 1983). The most fully expanded needles and leaves on the plants were sampled and the same individuals were measured each sampling day. Measurements were taken at the same position on the needles and leaves throughout the day. A constant leaf area of 400 mm^2 was measured on the *S. megaphylla* plants. *P. patula* needle surface area present in the cuvette was determined by a volumetric displacement technique (Johnson 1984).

3.5.2 Soil moisture profiles

The relationship between the amount of rainfall and drying out of the soil profile, and the variation in the pattern and rate of drying of the profile under different competition regimes, was studied. Soil moisture profiles which express the relationship between ϑ_s at different depths in the soil profile were determined for each treatment at two-monthly intervals from January 1989 until September 1989.

3.5.3 Water stress integrals

Most research on plant responses has been concerned with short term physiological responses such as plant water potential and stomatal conductance. Little attention has been paid to the longer term morphological responses. The relationship between plant water status and the growth or productivity of *P. patula* over time was determined by using the concept of a water stress integral $S\psi$. The water stress integral ($S\psi$) can be defined as the cumulative integral of pre-dawn leaf water potential over a set period of time (Myers 1988) and expressed as

$$S\psi = \left| \sum_{i=1}^{n} (\bar{\psi}_{i,i+1} - c) n \right| \qquad (15)$$

The same notation and method of calculation used by Myers (1988) was adopted, where $\psi_{i,i+1}$ is the mean ψ_{pine} or ψ_{grass} for any interval $i,i+1$, c is the maximum ψ_{pine} or ψ_{grass} measured during the study and n is the number of days in an interval. The maximum values for ψ_{pine} and ψ_{grass} were -0.2 and -0.1 MPa respectively. The date and frequency of the measurements are shown in Table 3.6.

Saturated hydraulic conductivity

The steady, gravity-induced, infiltration rate of water into a homogenous, structurally stable soil is comparable to the saturated hydraulic conductivity (Hillel 1980). Saturated hydraulic conductivity (K_{sat}), of the A and B horizons was determined using a constant head, shallow well permeameter (Amoozegar and Warrick 1986, Chappell 1992). Wells were cut into the soil using a cutting tool to avoid compaction, and measurements were made using de-ionised distilled water to simulate rainwater. Saturated hydraulic conductivity values were used in the water balance study to determine the relationship between θ_v and hydraulic conductivity.

Plant water potential

The differences in plant water potential in response to weed control have been extensively studied e.g. Lambert *et al.* (1972), Nambiar and Zed (1980), Sands and Nambiar (1983), and Lanini and Radosevich (1986).

The xylem pressure potential of *P. patula* needle fascicles (ψ_{pine}) and *S. megaphylla* leaves (ψ_{grass}) were measured using a pressure chamber (Tyree and Hammel 1972; Ritchie and Hinckley 1975; Cleary and Zaerr 1984). A stereo-microscope was used to view the cut ends of *P. patula* needle fascicles. As far as possible, only fully expanded needles were used. Two types of measurements were carried out, pre-dawn and diurnal. Three *P. patula* trees from each replication were selected for sampling. This resulted in a sample size of 72 needle fascicles per sampling period. A total of 60 *S. megaphylla* plants were also sampled on each occasion. As time became a serious constraint, pre-dawn sampling and storage was resorted to. Storage of needles prior to ψ_{pine} measurements has been reported by Ritchie and Hinckley (1975), Ritchie and Hinckley (1975), Kaufmann and Thor (1982), and Myers (1988). Pre-cooled glass test tubes with moistened sponges placed at the bottom and sealed with rubber stoppers were used to store the *P. patula* fascicles until they could be read later in the day.

S. megaphylla leaves were placed in polythene bags with moistened paper towelling. The samples were then placed in ice-filled cooler boxes until the ψ_{grass} readings could take place. A paired t-test, (SAS Institute Inc. 1987) was carried out to determine if any significant difference occurred in xylem pressure potential readings between pre-dawn and stored plants. No significant difference in ψ_{pine} occurred between the fascicles stored for up to eight hours and those where readings were taken immediately. Diurnal ψ readings took place the day after pre-dawn ψ readings and on the same day as stomatal conductance measurements.

$$\theta_{grav,s} = -58.6 + 377.3n \quad (14)$$

$r^2 = 0.63$
$n = 42$

for the B horizon. Gravimetric soil water content was then converted to volumetric water content (θ_s) by multiplying by the soil bulk density (Hanks and Ashcroft 1980).

Soil water potential

In order to characterize the soils of the trial, the relationship between the soil water content and the soil water potential (ψ_s) was investigated by developing soil water retention curves (Johnston 1989, Pearcy *et al.* 1989). Soil water retention curves for the A and B horizons were determined in the laboratory using the ceramic plate technique (Soil Moisture Equipment Co., Santa Barbara, California, USA). Soil samples were placed on a ceramic plate and a fixed suction or pressure applied to a given potential until no more water was forced out of the sample. The soil water content at that potential was then determined. At this point it is assumed that the water potential of the remaining soil water is approximately equal to negative of the pressure applied. Soil moisture characteristic curves for the A and B horizon are shown in Figure 3.6.

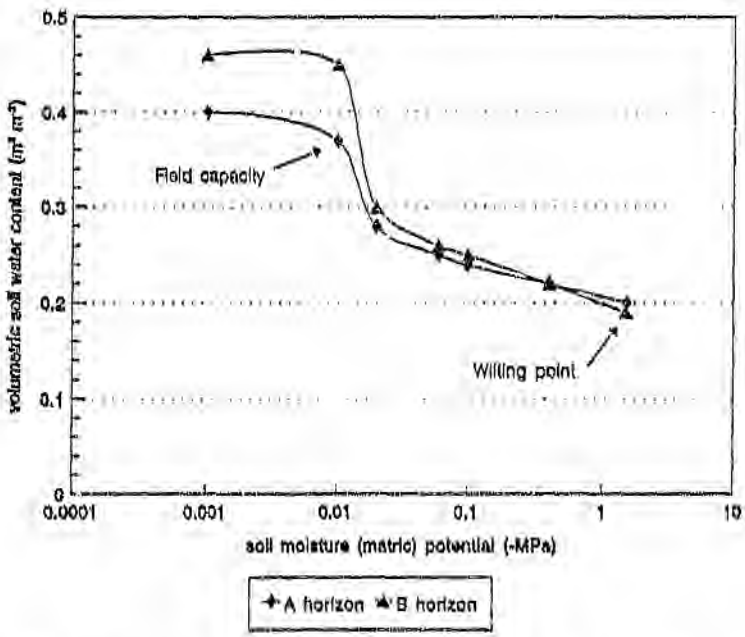


Figure 3.6. Soil moisture characteristic curves for the A and B horizons. The soil moisture potential scale is logarithmic and values are negative.

3.5 Soil and plant water moisture

The objective of the soil and plant water studies was to determine whether the growth of *P. patula* was limited by competition for water by *S. megaphylla*.

The following relationships were examined:

- monthly rainfall and its relation to soil moisture content under different competition regimes, and at different depths,
- the variation in soil moisture content with rooting density and extraction patterns for different treatments over time,
- the relationship between productivity and water stress, and
- the water balance of the different competition regimes.

3.5.1 Variables measured

Rainfall

Daily rainfall was recorded for a period of three years using a automatic tipping-bucket rain gauge (M.C. Systems, Plumstead, RSA). Daily rainfall was expressed on a monthly basis.

Soil moisture

Volumetric soil moisture content, (θ_v), was determined weekly from neutron probe readings (Series 3300, Troxler, NC., USA). One aluminium access tube was inserted in the centre of each treatment of each replication. Neutron count ratios were taken at 200 mm intervals up to a depth of 1.6 m. Count ratios were calibrated against gravimetric samples from both the A and B horizon. Gravimetric soil water content ($\theta_{grav,s}$), where n is the count ratio, was expressed as

$$\theta_{grav,s} = -43.3 + 436.9n \qquad (13)$$

$r^2 = 0.67$
$n = 42$

for the A horizon, and

$$k_c = \frac{y}{x^2 - h_c x} \tag{10}$$

Through determining the integral, the volume of the canopy is therefore:

$$V_c = \pi \left(\frac{k_c^2 x^5}{5} - \frac{2 k_c^2 h_c x^4}{4} + \frac{k_c^2 h_c^2 x^3}{3} \right) \tag{11}$$

Trees utilized in the biomass assessments (section 3.4.2) were also used in the light-use efficiency studies. Early growth was assumed to be exponential. Based on the measured needle mass, the $RGR_{w_{i\ needle}}$ (Equation 3), needle m .ss and leaf area increment were determined for the sample trees. Daily PAR was measured in the trial or obtained from the research centre weather stations situated 0.5 km away. PAR was recorded with quantum sensors (LI-190SB, Nebraska, USA). Where, data was missing due to sensor or data logger malfunction, the long term means were substituted. The amount of radiant energy absorbed was expressed as MJ m^{-2}. Biomass production included the root component and was expressed in g m^{-2}. The slope, ε, representing an estimate of light use efficiency, was determined for each treatment by means of linear regression.

The light-use efficiencies of *S. megaphylla* for treatments A, B, C and D were determined for the cumulative total biomass production as a function of radiant energy absorbed. After each clipping, the growth of the grass was assumed to be exponential. This is a fair assumption as the frequencies of clipping never allowed a sigmoidal type of growth relationship. The leaf areas of *S. megaphylla* were determined with a Delta T leaf area meter (Delta T Devices Ltd, Cambridge, UK). The relationship between the leaf area of *S. megaphylla* , $A_{Setaria}$ (m^2), and the leaf mass, $w_{l,Setaria}$ (kg), is

$$A_{Setaria} = 0.771 + 8.817 w_{l,Setaria} \tag{12}$$

$$r^2 = 0.91$$

$$n = 9$$

For *S. megaphylla* k=0.4 was used.

roles in the light interception process by influencing the amount of incoming shortwave radiation absorbed and its extinction through the canopy. As the time periods used in this study are long, there is little justification for using comprehensive canopy radiation interception models such as those defined by Norman and Jarvis 1974 and Oker-Blum *et al.* 1991. Therefore, canopy light interception was approximated using the Beer-Lambert law:

$$\varphi_{s,abs} = \varphi_s(1 - \exp(-kL) \quad (7)$$

where φ_s is the incoming shortwave radiation (PAR), k the extinction coefficient and L the leaf area index. For *P. patula* $k = 0.5$ was used .

In order to determine the leaf area index of the various layers of the canopy, it was necessary to determine the needle mass. It was assumed that there was a linear relationship between needle surface area and needle biomass. Total surface area of needles was calculated using the relationship:

$$A_{needle} = 32.2 + 124.0\ (W_{needle}) \quad (8)$$

$$r^2 = 0.93$$

$$n = 52$$

where A_{needle} is the total surface area of needles in cm^2 and W_{needle} is the mass of needles in grams (Dye 1993 *pers comm.*[2]). Projected area was calculated from total surface area by dividing by three (Johnson 1984). As the leaf area index of the canopy was known, the leaf area index for the individual canopy slices could be calculated by determining the volume of the canopy. By observation, it was assumed that the canopies of *P. patula* were roughly parabolic in shape. Biging and Wensel (1990) also found conifer profiles to be mainly parabolic.

The function

$$y = k_c\ (x^2 - h_c x) \quad (9)$$

describes a parabola where y is the maximum radius of the canopy, h_c is the height of the canopy and x is the height from the base of the canopy to a certain position within the crown. When $x = 0.5h_c$ then k_c is a species parameter determining the shape of the canopy profile. This function can be rewritten as:

[2] P. Dye, FORESTEK, Private Bag X11227, Nelspruit, 1200

Relationships were normalized and stepwise linear regression (SAS Institute Inc. 1987) was used to derive coefficients. Plots of residual versus predicted values for all significant variables were examined in order to graphically examine the adequacy of the regression models.

3.4 Light-use efficiency

Evidence from agricultural studies is that the rate of growth and production of a crop is proportional to the radiation intercepted (Monteith 1977). Numerous studies on plantation species have been carried out (e.g Cannell *et al.* 1987, Cannell *et al* 1988, Landsberg and Wright 1989, Dalla-Tea and Jokela 1991, Raison and Myers 1992) with respect to this relationship. The biomass production of *P. patula* under different competition regimes in relation to the amount of shortwave radiation, φ_s (0.4 0.7μm), was investigated by carrying out light efficiency studies.

Light-use efficiency, ϵ, can be defined as the slope of the linear relationship between dry matter production and the quantity of photosynthetically active radiation intercepted by the plant canopy. A detailed review on the analysis of forest production in terms of radiation utilisation efficiency has been carried out by Landsberg *et al.* 1995. They concluded that the ϵ is more than a coefficient of an empirical relationship and is based upon well understood physical and physiological processes.

The following relationships were examined:

- the variation in ϵ between treatments for *P. patula*,
- the variation in ϵ between treatments for *S. megaphylla*,
- the differences between ϵ of *P. patula* and *S. megaphylla*, and
- if differences between species occurred, the possible physiological reasons for them.

Light-use efficiency is given by the equation

$$W_T = \epsilon \sum \varphi_{s\,abs}(t)\Delta t \qquad (6)$$

where W_T is the net dry matter production, t is the time, ϵ the efficiency with which *P. patula* converts radiant energy (light), and $\varphi_{s,abs}$ the absorbed short-wave (0.4-0.7μm) radiation.

The amount and distribution of leaf area within the canopy and seasonal leaf dynamics play important

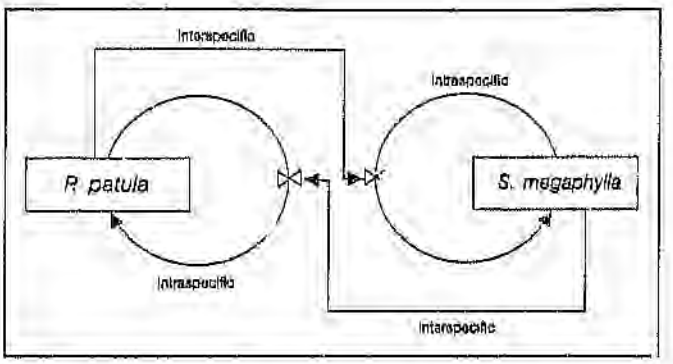


Figure 3.5. The competitive interaction between *P. patula* and *S. megaphylla*.

The growth of *P. patula* in the Control, with no *S. megaphylla* competition was assumed to be determined solely by environmental and site factors. The differences between the $RGR_{P,leaf}$ of the Control and the remaining treatments which were subject to the additional constraint of *S. megaphylla* competition were examined. When the difference at a particular time became negative ($RGR_{P,leaf}$ of the Control < $RGR_{P,leaf}$ of treatments) then it was assumed that interspecific competition was superseded by intraspecific competition. This occurred after approximately four months in treatment A, 15 months in treatment B, 15 months in treatment C and 17 months in treatment D. Only data prior to the above time periods were used in examing the interaction between *P. patula* and *S. megaphylla*.

An iterative process was followed to determine which variables had a significant impact on the foliage production of *P. patula*. The following relationships were examined:

- $RGR_{P,leaf} = f(\text{time})$,
- $RGR_{S,leaf} = f(\text{time})$,
- $RGR_{P,leaf} = f(W_{P,leaf}, W_{S,leaf})$,
- $RGR_{S,leaf} = f(W_{P,leaf}, W_{S,leaf})$,
- $RGR_{P,leaf} = f(RGR_{S,leaf})$.

Based upon the above relationships, an empirical competition model simulating $w_{P,leaf}$ in relation to $RGR_{P,leaf}$ when certain levels of *S. megaphylla* competition were imposed was developed using

- $RGR_{S,leaf} = f(W_{P,leaf})$ and
- $RGR_{P,leaf} = f(RGR_{S,leaf}, W_{S,leaf})$.

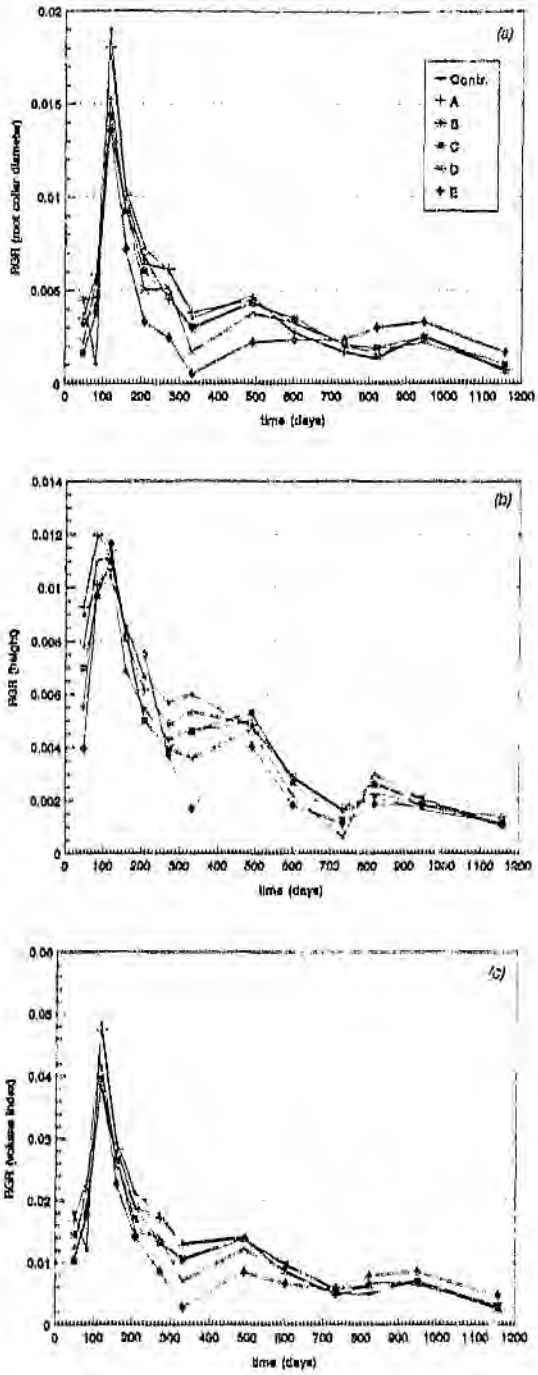


Figure 4.3. Relative growth rates measured at different intervals for (a) root collar diameter (cm cm^{-1} day^{-1}), (b) height (m m^{-1} day^{-1}) and (c) volume index (m^3 ha m^{-3} ha^{-1} day^{-1}) of *P. patula* growing under six different competition regimes.

period, the mortality of *S. megaphylla* increased from 0 to 13%, thereby reducing intraspecific competition. The variance in RGR_d between different treatments for different time intervals declined from a maximum at day 118. It is interesting to observe that at the 271 to 331 day interval, the RGR_d fell into four distinct clusters. The first cluster with the highest RGR_d includes the Control and treatment A. This is theoretically where competition from *S. megaphylla* is having the least impact. The second cluster includes treatment B and C. Clusters three and four contain treatments D and E respectively. The next interval displays three main groups. Cluster one contains the Control, treatments A, B and C, cluster 2, treatment D and cluster 3 treatment E. In the next interval, with the exception of treatment E, there was very little difference in the variance in RGR_d between the treatments. This could imply that with time, the various RGR_d of the treatments tend towards the RGR_d of the Control indicating a transition from interspecific competition between *P. patula* and *S. megaphylla* towards intraspecific competition between neighbouring *P. patula* trees. This implies that the competitive effect of *S. megaphylla* in treatment A lasted between approximately 271 and 331 days, treatment B and C between approximately 331 and 490 days, treatment D between 490 and 601 days and E between 601 and 734 days.

RGR_h at 118 days was greatest in treatment E and lowest in the Control (Figure 4.3b). Absolute height of E at this stage was also greater than that of the Control. The absolute mean heights of trees in treatment E were the greatest for the first eight months following establishment, whereafter their rate of growth declined. The greater heights recorded for treatment E until June 1989 could be ascribed to the fact that *S. megaphylla* canopy height in this treatment was greater than the tree height. For this reason, the trees allocated greater resources to height growth, at the expense of diameter growth in order to obtain apical dominance over competing *S. megaphylla*. Differences in PAR at the apical growing point of trees in treatment E for this period, (Figure 4.4), illustrate the possibility that shading was affecting growth. Cole and Newton (1986), studied the growth responses of *P. menziesii* to crowding and interspecific competition. They demonstrated that, although severe crowding decreases height growth, there was some evidence to suggest that a minor degree of 'crowding' may stimulate the allocation of resources to height growth.

Relative growth rates

The rates of growth for height, RCD and VI for the different treatments over a period of 3.16 years were highly significant with $F_{5, 600} = 16.07^{***}$ for height, $F_{5, 600} = 90.75^{***}$ for RCD and $F_{5, 600} = 61.56^{***}$ for volume index. For all three growth parameters, trees growing under the lowest competition regimes, namely the Control and treatment A, had significantly higher rates of growth than the remaining treatments. Treatments D and E, growing under the highest competition regimes, had the lowest rates of growth. Table 4.3 shows the degrees of significance between slopes for the different parameters and treatments.

Table 4.3. The growth rates (slopes of the log linear transformations) of *P. patula* for a period of 3.16 years. Vertical lines link treatments not significant at the 5% level and growth parameters are ranked from largest to smallest.

Height (m d^{-1})		Root collar diameter (cm d^{-1})		Volume index (m^3 d^{-1})	
A	0.0039	A	0.0038	A	0.0115
Contr	0.0038	Contr	0.0037	Contr	0.0113
B	0.0037	B	0.0036	B	0.0109
C	0.0036	C	0.0036	C	0.0108
D	0.0034	D	0.0034	D	0.0101
E	0.0033	E	0.0028	E	0.0089

When comparing rates of growth for a long intervals such as 3.16 years, it is likely that detailed growth and yield information will be subsumed. Relative growth rates at more frequent measurement intervals for RCD, (RGR_d) height (RGR_h) and volume index (RGR_{VI}) are illustrated in Figure 4.3. Generally the RGR_d, RGR_h and RGR_{VI} increased rapidly for the first four months following establishment, decreased exponentially for the next eight months and then gradually levelled off. The peaks in RGR for all three growth parameters could be associated with seasonal influences such as increased temperature and rainfall. The response in RGR for the 332 to 490 day and 820 to 947 day intervals for all treatments including the Control (no *S. megaphylla* competition) were not as marked, compared to the 82 to 118 day interval. This is despite the fact that the amount of rainfall, (Figure 4.19), that fell during the latter two periods was greater than the long term-monthly average. This suggests that other factors are reducing the RGR. These could be intraspecific competition, or rainfall interception losses as a result of progressively greater leaf areas.

RGR_d and the variance in RGR_d between different treatments altered with time (Figure 4.3a). Generally the RGR_d reflected the different competition regimes, with the RGR_d of the Control and treatment A being greater than the remaining treatments. Except for treatment E, RGR_d for all treatments decreased for the intervals from day 490 to day 820. Treatment E had the lowest RGR_d until the 601 to 734 day interval. Thereafter it increased, and remained the highest. A possible explanation is that the trees in treatment E had then attained a size where they could outcompete *S. megaphylla*. In addition, for this

Table 4.2. The percentage survival and number of stems per hectare of *P. patula* for the six competition regimes 3.16 years after planting.

Treatment	% Survival	S ha^{-1}
Control	99	1358
A	98	1344
B	98	1344
C	100	1372
D	97	1331
E	87	1193

Needle growth was significantly different between treatments over time ($F_{5,10} = 6.82^{**}$). This relationship for the different treatments can be best described by the negative exponential curves illustrated in Figure 4.2. 120 days after bud initiation the mean length of needles in the Control (187 mm) was significantly greater than in the remainder of the treatments. Mean needle lengths in treatments A (147 mm), B (122.5 mm), D (115.5 mm) and C (113.3 mm) were also significantly greater than in treatment E (78 mm). Needle elongation ceased in treatment E 50 days after bud initiation, whereas elongation growth in the remaining treatments plateaued off at 90 to 100 days after initiation. Field observations indicated that the needles of trees in treatment E were thin and chlorotic in colour.

Similar trends were observed with *P. taeda* where seedlings grown with no interfering vegetation had greater needle lengths than those growing with herbaceous competition (Zutter *et al.* 1987). Nambiar and Zed (1980) found that the length of fascicles of *P. radiata* increased markedly as the intensity of weed control increased.

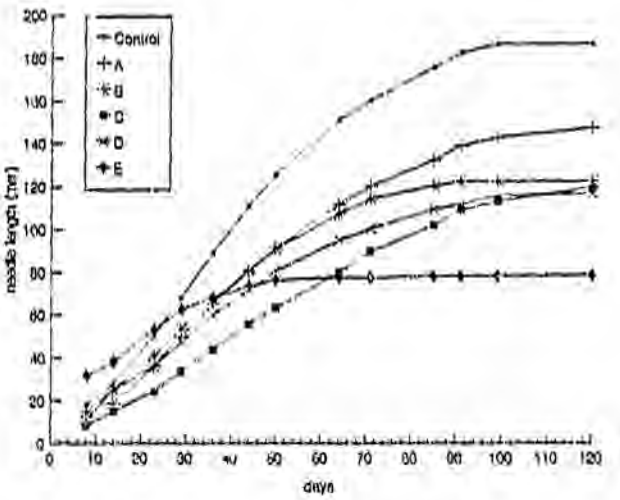


Figure 4.2. Needle lengths of *P. patula* growing under six different competition regimes.

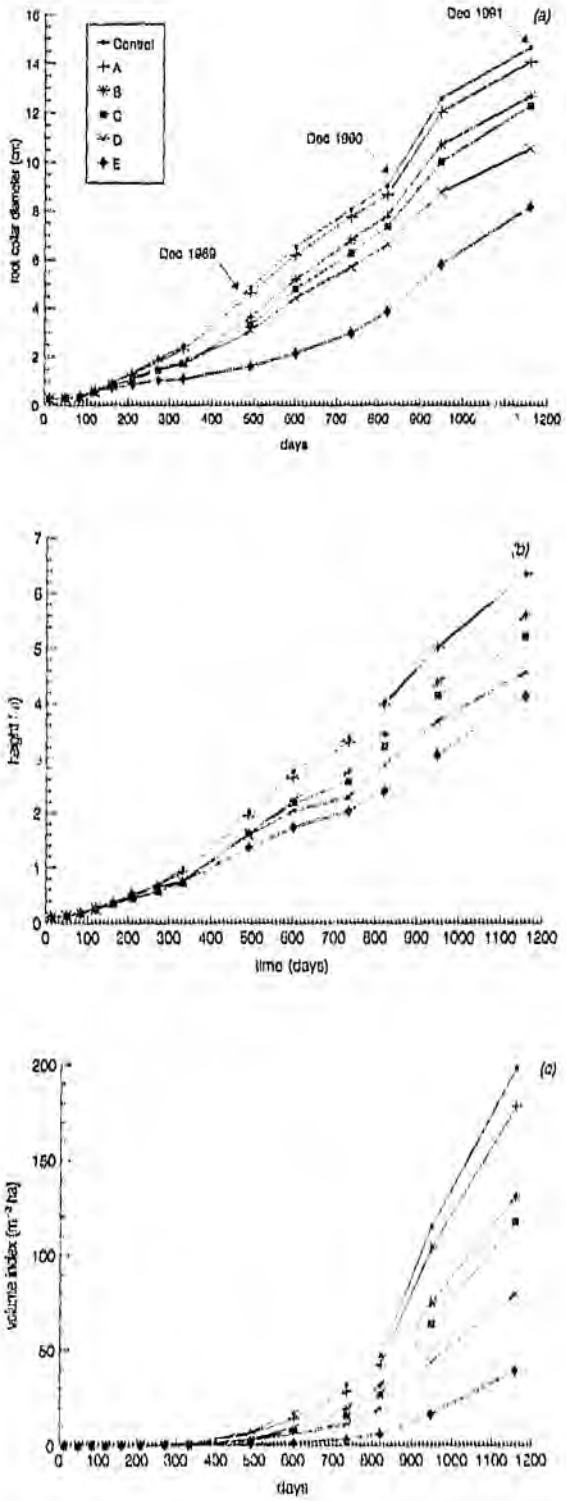


Figure 4.1. Mean root collar diameter (a), height (b) and volume index (c) of *P. patula* growing under six different competition regimes. Control = lowest competition regime and E = highest competition regime.

4. RESULTS AND DISCUSSION

4.1 Growth and yield

4.1.1 Absolute growth and relative growth rates of *P. patula*

Absolute growth

Height, RCD and volume index for *P. patula* are illustrated in Figure 4.1. Growth is exponential and reflects the six *S. megaphylla* competition regimes. The mean heights, RCD's and volume indices 3.16 years after establishment are shown in Table 4.1. At this age, differences between treatments for these three growth parameters were highly significant with $F_{5, 570} = 73.16^{***}$[4] for height, $F_{5, 570} = 84.75^{***}$ for RCD and $F_{5, 570} = 91.91^{***}$ for volume index. The sample size, mean, standard deviation and standard error for these growth parameters are presented in Appendices 1 to 3. The mean heights of the trees in the Control and treatment A, were approximately 35% greater than the mean height of trees in treatment E. Heights ranged from 4.1 m in the highest competition regime (treatment E) to 6.4 m in the Control, a difference of 2.2 m. RCD was greatest in the Control, (14.7 cm), and treatment A, (14.1 cm), and lowest in treatments D (10.6 cm) and E (8.2 cm). Volume index exhibited the same trends as height and RCD.

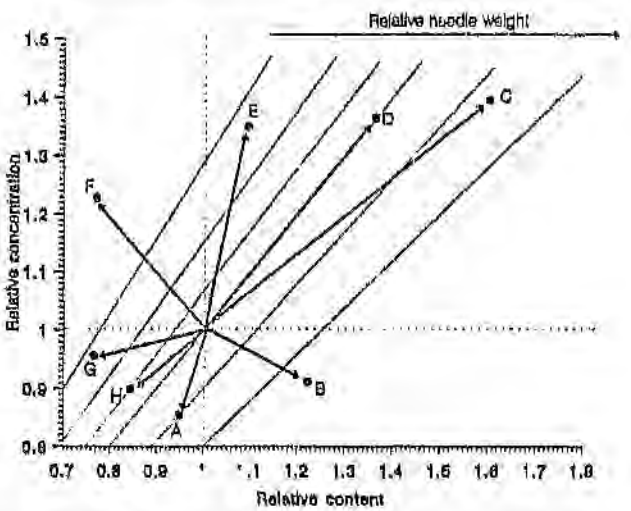
Table 4.1 The mean height, root collar diameter and volume index of *P. patula* evaluated at the age of 3.16 years. Vertical lines link treatments not significant at the 5% level and growth parameters are ranked from largest to smallest.

Height (m)		Root collar diameter (cm)		Volume index (m^3)	
Contr	6.4	Contr	14.7	Contr	196
A	6.3	A	14.1	A	178
B	5.6	B	12.7	B	131
C	5.2	C	12.3	C	117
D	4.6	D	10.6	D	79
E	4.1	E	8.2	E	39

Tree survival, 3.16 years after establishment is illustrated in Table 4.2. Based on a planting espacement of 2.7 x 2.7 m, survival was highest in treatment C (100%) and lowest in treatment E (87%). Survival in treatment E was significantly different to the rest of the treatments.

[4] Significant at the: *** (1%), ** (5%), * (10%) level.

Table 3.7. An interpretation of possible vector analysis for trees to explain competition effects as a result of changes in nutrient concentration, nutrient content and needle mass. A zero (0) indicates no change while a positive (+) or a negative (-) indicate an increase or decrease respectively in either concentration, content or mass.



Vector shift	Nutrient		Relative needle mass	Competition effects	Moisture regime
	Relative conc.	Relative content			
A	-	0/+	+	Growth improved. Nutrient not limiting (dilution may occur).	Moisture stress reduced
B	-/0	+	+	Growth improved. Greater nutrient availability.	Moisture stress reduced
C	+	+	+	Growth improved. Competition reduced all stresses a. increased nutrient availability.	Moisture stress probably reduced
D	+	+	0	No growth change. Nutrient not limited by competition and accumulation occurring.	Moisture non-limiting
E	+	0/+	-	Growth reduced. Nutrient not limited by competition and accumulation may occur.	Moisture stress induced by competition (allelopathy or nutrient may be possibly reducing growth).
F	+/0	-	-	Growth reduced. Nutrient uptake but not concentration reduced by moisture stress. Nutrient not limited by competition.	Moisture limiting growth
G	-	-	-	Growth reduced. Nutrient limiting growth as well as moisture.	Moisture limiting growth as well as nutrient
H	-	-	0	No growth change. Lower nutrient status indicates plants without competition had luxury nutrient consumption.	Moisture not limiting

The method is based upon the principle that significant changes in nutrient concentration, nutrient content and needle mass will occur under different competition regimes and that both nutrient and moisture status are therefore likely to differ. The technique involves the construction of vector diagrams or graphs which illustrate foliar concentration *versus* foliar nutrient content *versus* needle mass. All concentrations, contents and masses are expressed relative to a control.

The September 1989 foliar nutrient concentrations for each treatment were used. Needle biomass was utilized as the measure of productivity. This was determined using Equation 4. Changes in the nutrient concentration, nutrient content and needle mass of treatments A, B, C, D and E relative to the Control were plotted on graphs, and vectors drawn between the Control and the nutrient elements. Interpretations of the direction and magnitude of the vectors were then used to determine the impact various competition regimes have on the nutrient status and growth of the trees. A diagnostic interpretation of the vectors is given in Table 3.7. Movement of a vector (vector shift) could be in eight possible directions (A to H). Any one of the eight possible shifts of the vector would be as a result of competition for nutrients, or for moisture, or both. As an example, in vector A, the relative needle mass is positive without any significant change in the relative nutrient concentration. This indicates that nutrients are most probably not limiting and that there is a favourable moisture regime. It can also be inferred that, should there be a decrease in either nutrient concentration or content, and needle mass also decreases, moisture stress is likely to have occurred.

3.6.2 Vector Analyses

The foliar nutrient studies provide scant information on the nutrient dynamics of the competition trial. For instance, the frequency of foliar sampling was insufficient to determine, how the foliar nutrient status fluctuated with time, needle age, position in the canopy, or plant water status. In an attempt to relate available foliar nutrient data to a measure of productivity, vector analyses were used.

The principle of vector analysis is based on changes that occur in the nutrient concentration, nutrient content and needle mass in the foliage of trees that have undergone specific silvicultural treatments. This approach could prove useful in studies involving competing vegetation (Mead and Mansur 1993). The technique is fully described by Wheetman (1989) and could be useful in

- assessing post establishment responses to various silvicultural prescriptions,
- determining the nutritional status of trees relative to a control,
- forecasting subsequent growth responses to silvicultural treatments, and
- assessing the effect of interspecific competition (Mead and Mansur 1993).

The theory is based on the yield curve (Timmer and Morrow 1984). The curve (Figure 3.7) illustrates a measure of productivity (e.g., biomass) as a function of nutrient concentration. The curve contains three distinct phases. The first phase is from point a to b and represents the zone of deficiency where increases in foliar concentrations result in increases in growth. Point b is the critical level. Beyond this point little additional growth will occur in responses to increases in foliar concentrations and consumption of nutrients is regarded as luxury. The decline in growth (phase c to d associated with an increase in nutrient levels signifies toxicity.

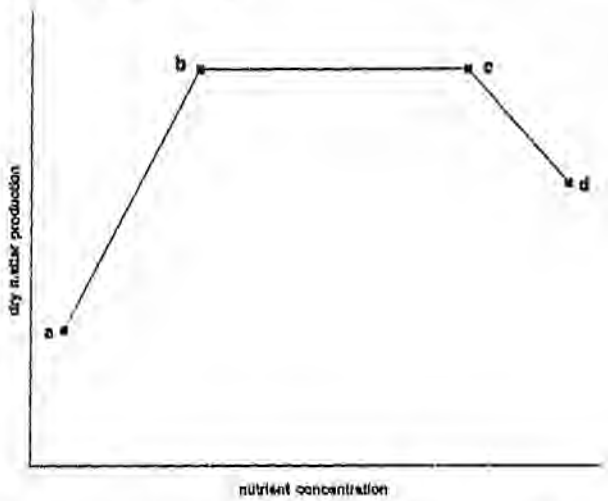


Figure 3.7. A yield curve demonstrating needle biomass as a function of nutrient concentration.

3.6 Foliar and soil nutrients

3.6.1 Foliar and soil nutrient analyses

Paired comparisons of soil and foliar nutrients were made to monitor the change in the nutrient status of the different competition regimes over time. Foliar sampling of *P. patula* and *S. megaphylla* took place in winter, the most stable sampling period (Payn *et al.* 1989). September 1989 results were compared with those of July 1990 (SAS Institute Inc. 1987). ANOVA was used to test for differences in soil and foliar nutrient status between the different competition regimes 21 months after establishment.

Foliar samples were oven-dried at 65 °C for two days and acid digested with sulphuric acid using lithium and selenium as catalysts (Nicholson 1984). Analyses of Ca and Mg were carried out by atomic absorbtion, K and Na by flame photometry and P and N by colorimetry. Calibrations were checked using standard samples of known concentrations and reported as mg kg^{-1}.

To determine available Ca, Mg, Na and K in the soil, weighed, oven-dried samples were extracted with ammonium sulphate (pH 5) and cations determined by atomic absorbtion for Ca and Mg, and by flame photometry for K and Na. Total N was determined by acid digestion followed by colorimetric determination. Results are reported as $\mu g\ g^{-1}$. Available P was assessed by extracting soil with Bray solution (ammonium fluoride or hydrochloric acid) and determined using colorimetry. To determine total P using colorimetry, soil samples were digested using nitric or perchloric acid. Results for both P (Bray 2) and total P are expressed as $\mu g\ g^{-1}$ (Black *et al.* 1965).

The N-mineralization rates of the soil were also determined, as total N provides little information on N availability and uptake. An *in situ* incubation technique was used to measure the rate of N-mineralization in each treatment in each replication. 50 mm diameter polyvinyl chloride (PVC) tubes were driven into the soil to a depth of 150 mm. The soil encapsulated by each tube was then watered and left to incubate for a period of two weeks (*t14*). At the time of tube insertion, and adjacent to each tube, a soil sample was taken to determine background mineral-N concentrations (*t0*). The determinations of NH_4^+ and NO_3^- were done according to the standard methods described by Anderson and Ingram (1989). The amounts of NH_4^+ and NO_3 were calculated as μg N g^{-1} of soil and the rate of N-mineralization were calculated as follows:

$$\Delta N_{mineralisation} = \frac{[(Nitrate_{t\,14} - Nitrate_{t\,0}) + (Ammonium_{t\,14} - Ammonium_{t0})]}{time} \qquad (15)$$

$$Weighted\ \theta_{soil} = RootProportion(\theta_{soil} - \theta_{wp}) \quad (28)$$

The conductance (g_c) of either the *P. patula* or *S. megaphylla* canopy is

$$g_c = g_{ref} L^* (Weighted\ \theta_{soil}) \quad (29)$$

where g_{ref} is the maximum stomatal conductivity and L^* the leaf area index. The product of the output of Equation 18 and g_c provides an estimate of transpiration.

3.5.5 Water-use efficiency

The ratio of net assimilation to transpiration is regarded as water use efficiency (WUE). The definitions of assimilation, transpiration and WUE differ. For example, assimilation might be expressed as net CO_2 exchange, dry matter growth or yield or economic yield. Gas exchange studies to investigate WUE are the most numerous. As examples, Sheriff *et al.* (1986) examined the the relationship between nutrient status, carbon assimilation and WUE in *P. radiata*. Aussenac *et al.* (1989) studied water use efficiency and drought tolerance in *Pseudotsuga menziesii* and *P. macrocarpa*, and a similar study was carried out by Gross (1989) on *P. menziesii* and *Picea abies*. Jarvis (1986) compared *Picea sithchensis* evaporation assimilation ratios (E/A) to those of agricultural crops. He concluded that there is a great need to measure E/A of stands in relation to nutrient and water stress. The relationship between the carbon isotope ratio and the intracellular CO_2 concentration (c_i) is also related to water use efficiency (Pearcy *et al.* 1989). Water loss may be expressed as either water transpired or total evaporation.

In this study the water use efficiency of *P. patula* and *S. megaphylla* under different competition regimes was examined. The total biomass production of *P. patula* (*W*) and the aboveground biomass of *S. megaphylla* were compared to the respective species cumulative transpiration rates. Biomass was expressed in g ha^{-1} and cumulative transpiration (E_T) converted from depth equivalents to mass per unit area units (kg ha^{-1}).

(θ_i) either at field capacity, wilting point, at the critical level, or where stomatal closure occurs, can be determined by:

$$\theta_i = \theta_i (\theta_{sat} - \theta_{ad}) + \theta_{ad} \quad (25)$$

The actual calculations in the model are conducted using the depth equivalent of water in each soil layer (d_i), where:

$$d_i = \theta_i z_i \quad (26)$$

and z_i is the thickness of the soil layer and θ_i the volumetric water fraction.

The model is limited to stands with rooted soil profiles that are not supplied with water from a water table with capillary rise. If the infiltrated water plus the amount of water stored in the rooted zone exceed the maximum soil moisture that can be held in the soil matrix suction against gravitational force (which state is, by definition, equal to field capacity), the model arranges for the surplus to be drained to the deep underground. Drainage cannot exceed the limits set by the hydraulic conductivity of the soil.

If rainfall rate exceeds the rate at which water can infiltrate the soil, which in turn is determined by the saturated hydraulic conductivity (K_{sat}) of the soil, run-off will occur. Run-off is usually related to the surface of the soil. However, the lateral flow of water within a horizon is also regarded as run-off. This occurs when the soil water content of a profile is greater than the saturated soil water content.

In order to calculate the evaporation for *P. patula* and *S. megaphylla*, the root weighted soil water content for the two species were determined. The proportion of *P. patula* and *S. megaphylla* roots in the soil profile was determined from the root distribution study. If the soil water content (θ_{soil}) is greater than the wilting point (θ_{wp}) and the critical level where stomatal closure occurs (θ_{crit}) then the weighted soil water content is expressed as:

$$Weighted\ \theta_{soil} = RootProportion(\theta_{soil} - \theta_{wp}) \quad (27)$$

If the soil water content (θ_{soil}) is less than the critical level where stomatal closure occurs (θ_{crit}) then the weighted soil water content is:

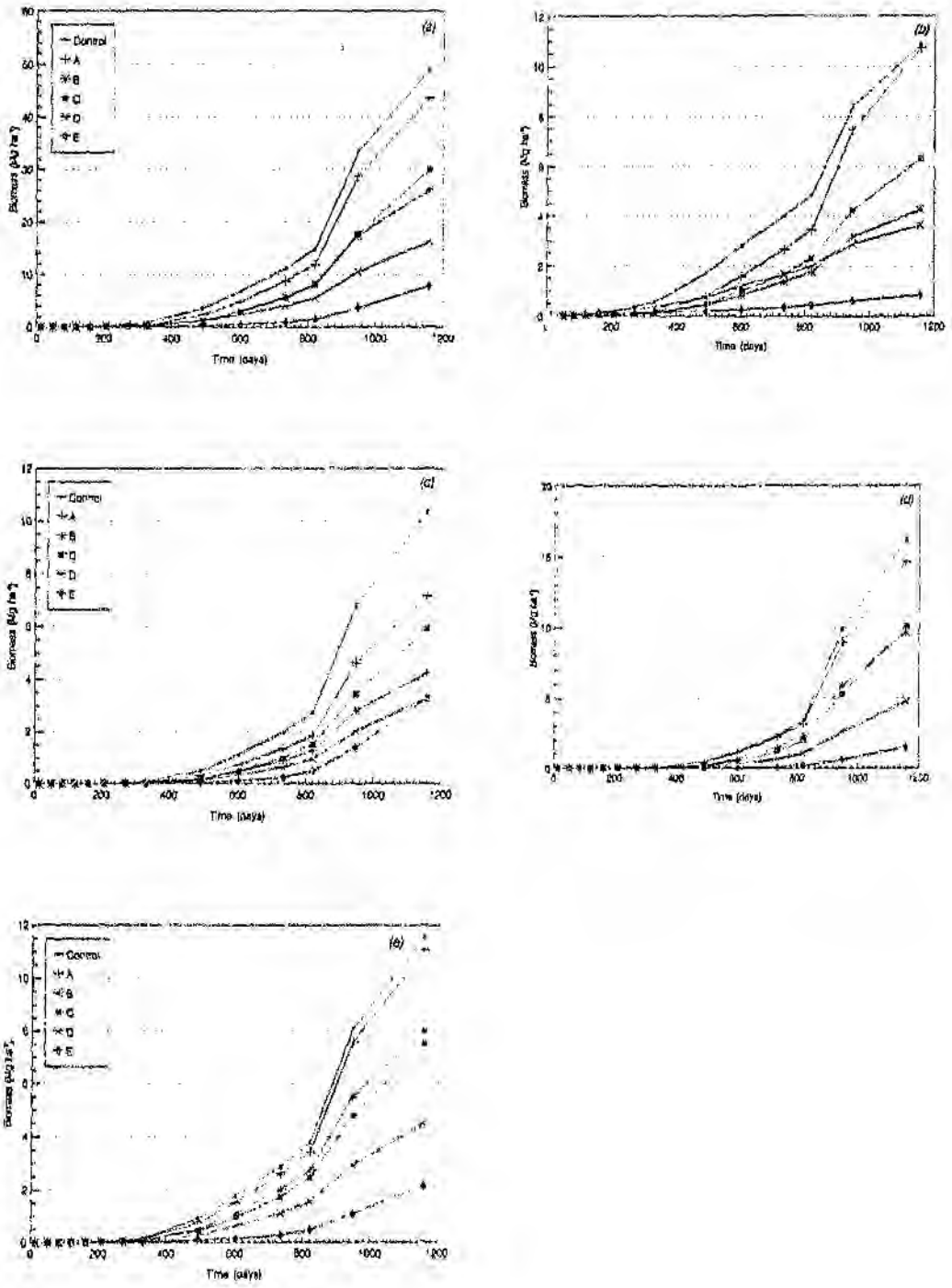


Figure 4.8. The *(a)* total, *(b)* root, *(c)* stem, *(d)* branch and *(e)* needle biomass production for *P. patula* over time.

Figure 4.8 shows the total, root, stem and branch biomass production for *P. patula* over time. For all biomass components, production was clearly exponential and reflected the various competition regimes. Differences in the total biomass 3.16 years after planting were highly significant ($F_{5, 577} = 80.8^{***}$). The Control was significantly different to all treatments and treatment A was significantly different to treatments B, C, D and E. No significant difference in aboveground biomass occurred between treatments B and C although they were significantly different to treatments D and E. By December 1991, (1157 days after establishment), Control and treatment A had attained a mean biomass of approximately 38 and 34 Mg ha^{-1} respectively, while treatment E was 78-81% lower at approximately 7.4 Mg ha^{-1}.

The differences between treatments for the root ($F_{5, 577} = 192.5^{***}$), stem ($F_{5, 577} = 54.0^{***}$), branches ($F_{5, 577} = 66.7^{***}$) and needle biomass ($F_{5, 577} = 81.2^{***}$) components were all significant. Generally the trends observed for total biomass were reflected in each of the components. The Control and treatment A produced the greatest biomass and treatment D and E the second lowest and lowest respectively.

4.1.2 The biomass of *P. patula*

The allometric equations defining the relationship between the independent variable, d_c, and the biomass of roots, stems, branches or needles, (w_i), for the various treatments are presented in Table 4.7. The pooled allometric equations where all treatments are combined is also included.

Table 4.6. The allometric constants (n_i) and coefficients (a_i) for the allometric equation $\ln w_i = a_i + n_i \ln d_c$, where w_i is the biomass of the roots, stems, branches or needles and d_c is the root collar diameter.

Biomass component	Treatments	ai	n_i	R^2	SE
Roots (g m^{-2})	Control	-1.26	1.65	0.70	9.62
	A	-4.50	2.32	0.91	5.19
	B	-2.70	1.81	0.65	14.26
	C	-2.98	1.96	0.80	8.77
	D	-0.06	1.28	0.55	12.78
	E	0.70	0.85	0.34	9.14
	Pooled	-1.76	1.67	0.69	77.97
Stems (g m^{-2})	Control	-4.716	2.737	0.97	1.84
	A	-5.272	2.800	0.98	1.53
	B	-4.066	2.503	0.97	1.61
	C	-4.360	2.645	0.99	0.49
	D	-4.401	2.521	0.96	2.69
	E	-3.547	2.606	0.98	0.99
	Pooled	-4.024	2.554	0.98	17.87
Branches (g m^{-2})	Control	-6.651	3.215	0.92	7.92
	A	-6.327	3.158	0.98	1.71
	B	-5.789	3.029	0.97	2.04
	C	-6.267	3.147	0.98	2.23
	D	-6.912	3.241	0.96	4.43
	E	-5.776	2.935	0.96	2.72
	Pooled	-6.296	3.187	0.96	24.1
Needles (g m^{-2})	Control	-2.464	2.308	0.93	3.49
	A	-2.926	2.414	0.98	0.95
	B	-2.158	2.240	0.97	1.07
	C	-1.861	2.176	0.99	0.31
	D	-2.383	2.255	0.97	1.38
	E	-1.647	2.076	0.99	0.46
	Pooled	-2.157	2.333	0.97	9.51

The differences in the allometric constant, n_i, between the different treatments and for the different biomass components indicates that the allocation of biomass differs under different competition regimes. It is difficult to detect any clearcut trends, and the allometric relationships may be confounded by the small sample size (Table 3.5). For treatment E, the allometric constant is lowest for root, branch and needle biomass, and the second lowest for stem biomass. The allometric constant for stem, branch and needle biomass is the highest or second highest in the Control.

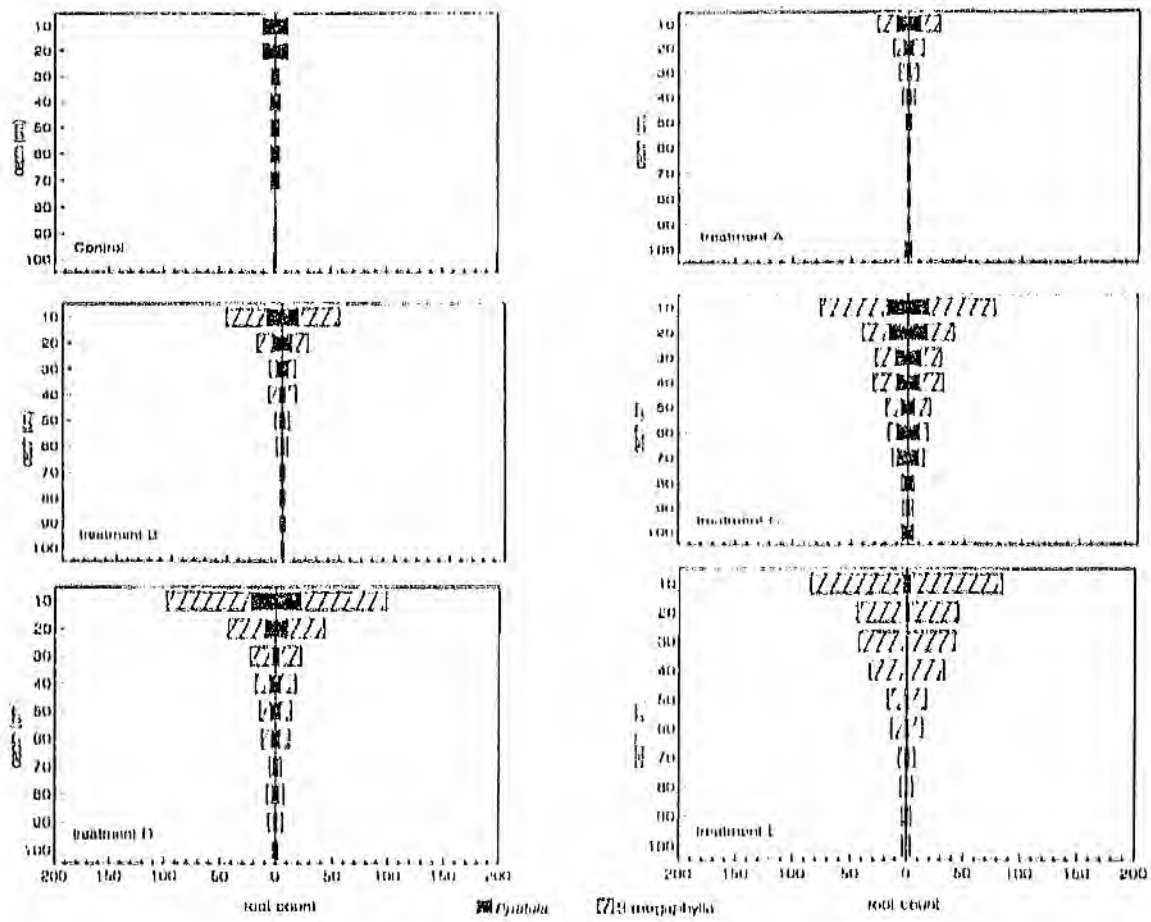


Figure 4.7c. The root distribution patterns for P. patula and S. megaphylla through the soil profile for the Control and treatments A, B, C, D and E, thirty two months after establishment.

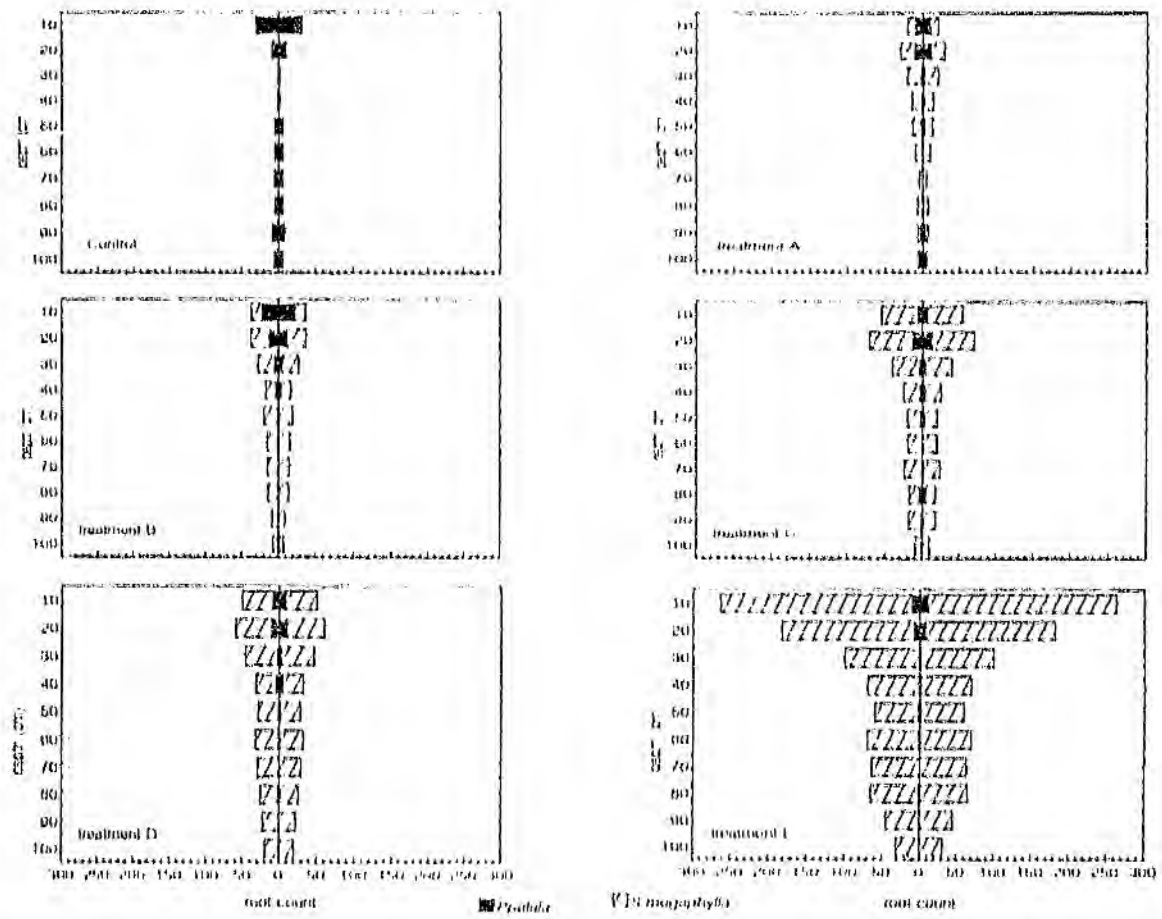


Figure 4.7b. The root distribution patterns for *P. patula* and *S. mogaphylla* through the soil profile for the Control and treatments A, B, C, D and E, twenty months after establishment.

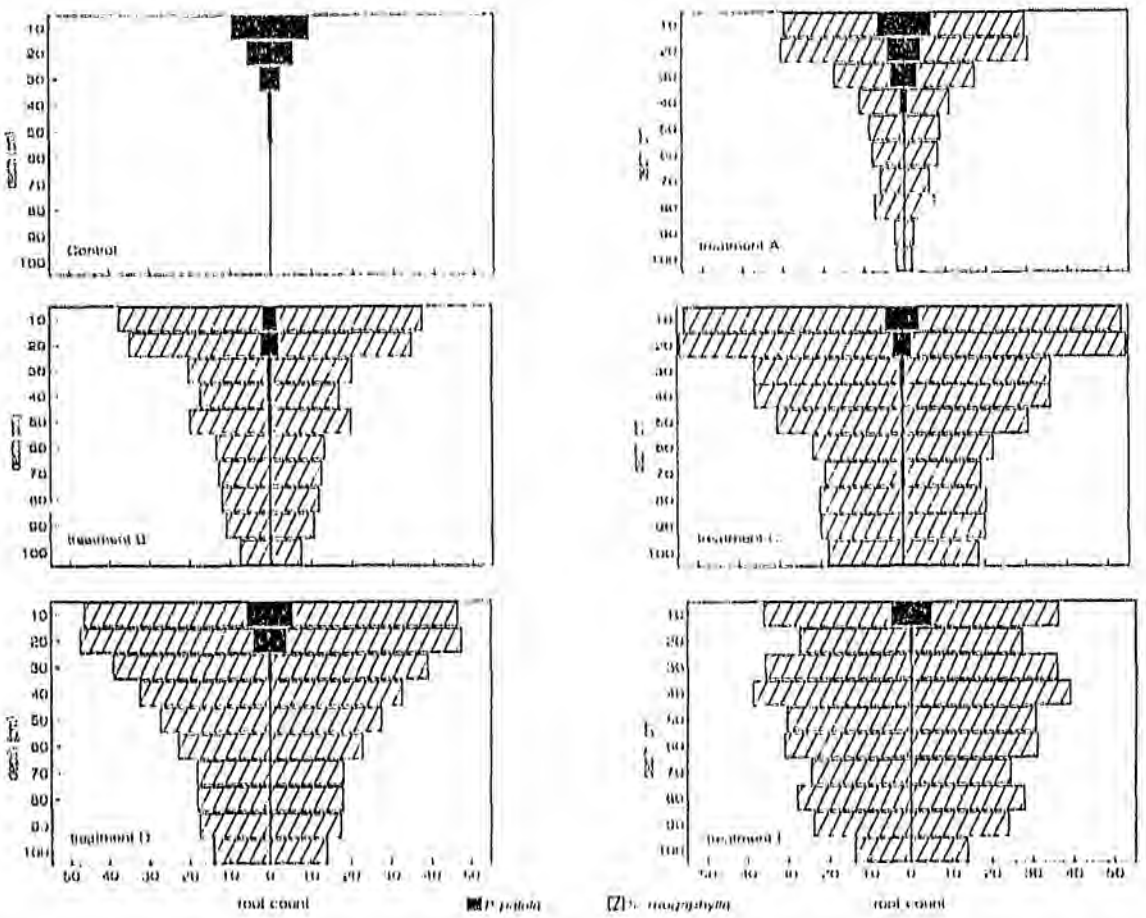


Figure 4.7a. The root distribution patterns for *P. patula* and *S. megaphylla* through the soil profile for the Control and treatments A, B, C, D and E, six months after establishment.

Table 4.5. Mean root masses (g m^{-2}) of *P. patula* and *S. megaphylla* 32 months after establishment. Vertical lines link treatments not significant at the 5% level.

P. patula						*S. megaphylla*	
fine		coarse		total		total	
D	23.2	Contr.	1575.8	Contr.	1595.4	E	254.6
Contr.	19.6	A	898.6	A	914.9	D	183.8
A	16.2	C	782.2	C	798.2	C	108.7
C	16.1	B	686.2	B	702.0	B	75.1
B	15.8	D	672.4	D	695.6	A	25.6
E	9.9	E	146.3	E	156.1	Contr.	0

There is a paucity of information on the root biomass of *P. patula*. Besides this study, only Morris (1992) has carried out root studies on *P. patula*. Morris (1992) developed a regression equation describing the relationship between coarse or structural roots greater than 20 mm in diameter, and diameter at breast height and height. This equation was not suitable for this study as the trees had not attained heights suitable for diameter at breast height measurements, and fine roots were not considered.

Figures 4.7 a, b and c reflect the root distribution pattern through the soil profile six, 20 and 32 months after establishment. These figures show that, as the intensity of *S. megaphylla* competition increased, the root count increased. The root count for *S. megaphylla* in treatment E was highest 20 months after establishment, and thereafter decreased. Generally, the converse occurred with *P. patula*. Of interest is the root count of *P. patula* in treatments B, C and D, 32 months after establishment. Their respective root counts are higher than in the Control and treatment A, even though aboveground biomass is less. One might hypothesize that, as a result of higher competition levels, and the need for the roots to colonize a greater soil volume in order to acquire limited water and nutrients, the allocation of biomass is skewed towards the root system at the expense of aboveground biomass. The far higher *S. megaphylla* root counts in all treatments is a clear indication of the vigour of this grass species. 32 months after establishment, between 38 and 70% of *P. patula* roots occurred in the top 300 mm of soil, with few roots penetrating deeper than 500 mm. The percentage of *S. megaphylla* roots in the top 100 mm of soil was greater than that for *P. patula* and ranged from 66 - 88%.

The results of *P. patula* root distribution are consistent with those reported elsewhere in the literature. Namblar (1963), working with young *P. radiata* in South Australia, found that 80-90% of lateral roots occured in the top 300 mm of soil. Squire *et al.* (1978) report on a number of workers who have examined the spatial distribution of pine root systems. Their results are remarkably consistent, and show that root concentration declines slowly with soil depth and is particularly high in the top 250 mm of soil. Bowen (1964) in Squire *et al.* (1978) examined root distribution of *P. radiata* in South Australia and found from 52 -84% by weight of roots in the top 250 mm. Squire *et al.* (1978) found *P. radiata* roots mainly in the top 115 mm of soil.

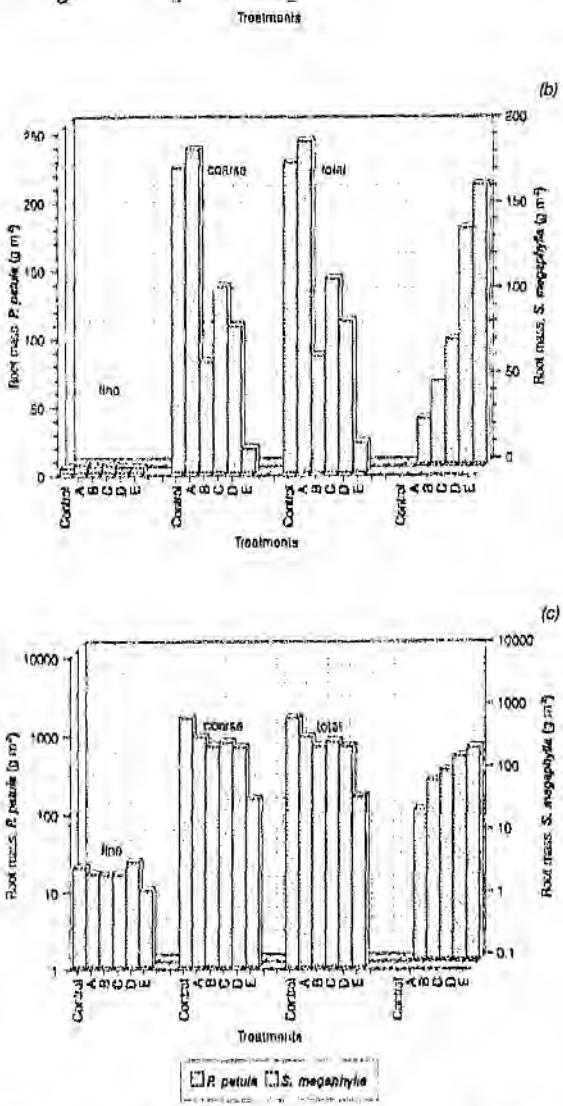


Figure 4.6. The root masses (g m^{-2}) of *P. petula* and *S. megaphylla* measured (a) 6, (b) 20 and (c) 32 months after establishment.

The root masses of *P. patula* and *S. megaphylla* 6, 20 and 32 months after establishment are illustrated in Figure 4.6. Means and standard deviations of root masses for the various treatments are presented in Appendix 5. Six months after establishment (Figure 4.6a), no clear trend in the total root mass of *P. patula* was evident. The Control (39 g m^{-2}) had a higher mass compared to the remaining treatments. Unlike fine root density, fine root mass only contributed between 6 and 33% to the total root mass of *P. patula*.

As with root density, the mass of *S. megaphylla* roots followed the same trend as reflected by the clipping regime. Six months after establishment, treatment E had the greatest mass (59 g m^{-2}) and treatment A the lowest (17 g m^{-2}). The contribution of *P. patula* total root mass to the total combined root mass of *P. patula* and *S. megaphylla* was far higher than for root densities, ranging between 20 and 44%, depending on the treatments. This is clearly indicated in a paired t-test which shows that no significant differences occurred in total root mass between the two species ($t_{(2)48}$ = 1.27). The probable reason for this is the large contribution that the coarse component makes to the total root mass of *P. patula*.

Twenty months after establishment (Figure 4.6b) treatment A (244 g m^{-2}) had the highest root mass and treatment E (22.4 g m^{-2}) the lowest. Fine root mass only contributed from 2.6 to 17% of the total mass. The mass of *S. megaphylla* roots was greatest in treatment E (163.7 g m^{-2}) and lowest in treatment A (26.9 g m^{-2}). *P. patula* total root mass comprised 12 to 90.1% of the combined root mass of *P. patula* and *S. megaphylla*. This was higher than the contribution of *P. patula* to the combined root densities.

Thirty two months after establishment (Figure 4.6c), the total root mass of *P. patula* was greatest in the Control (1595 g m^{-2}), and least in treatment E (156 g m^{-2}). The differences between these two treatments were significant (Table 4.5). The contribution of fine root mass to the total root mass ranged from 1.2 to 6.3%, which was substantially less than the contribution of fine root density to total root density. The greatest root masses for *S. megaphylla* occured in treatment E (255 g m^{-2}). This mass was significantly different to the root masses of treatment A (26 g m^{-2}), B (75 g m^{-2}) and C (109 g m^{-2}). The root mass of *S. megaphylla* contributed far less to the combined root masses of *P. patula* and *S. megaphylla* (Table 4.5). The contribution ranged from 2.7% in treatment A to 62% in treatment E. Nambiar (1983) found that rooting densities in two-year old *P. radiata* plantations were low (500 - 3200 m m^{-3}). He also found that roots less than 1 mm in diameter contributed 87.3 and 85.5% of the total root length at 34 and 46 months respectively, but only 38.9 and 22.2% of the mass.

highly significant ($t_{(2)49} = 7.15^{***}$). The relative differences in root density between *P. patula* and *S. megaphylla* were maintained over time. Twenty months after establishment (Figure 4.5b), the fine root density of *P. patula* ranged from 154 to 257 m m^{-3} for treatments E and A respectively. The differences in fine root density between the treatments was not significant. Coarse and total root densities of *P. patula* followed similar trends to that of fine roots although the root density in treatment A was significantly less than in treatment E. The contribution of fine roots to total length ranged from 54 to 73%.

For the same period, the root density of *S. megaphylla* in treatment E, was the greatest (8137 m m^{-3}), while the density in treatment A was the lowest (1672 m m^{-3}). The rooting density of *S. megaphylla* in treatment E was significantly different to the remaining treatments. The total root densities of *P. patula* for the different treatments only contributed 2.6 to 20.2% of the combined root density of both *P. patula* and *S. megaphylla* .

In 1991, 32 months after establishment, the fine root densities of *P. patula* ranged from 362 m m^{-3} to 719 m m^{-3} (Figure 4.5c and Table 4.4). The fine root density of *P. patula* in the Control was significantly greater than in treatment E. Differences in fine root density of *P. patula* were not significant for the remaining treatments. The contribution of fine root density to the total density of *P. patula* roots ranged between 34 and 50%. The contribution of fine root density to the total density of *P. patula* roots increases as competition increases.

Table 4.4 also shows the root density of *S. megaphylla* 32 months after establishment. The root densities of *S. megaphylla* are consistent with those recorded 20 months after establishment indicating that competition regimes were similar and had stabilized. *S. megaphylla* root density in treatment E (8785 m m^{-3}) was significantly greater than the Control, treatments A (1026 m m^{-3}), B (2597 m m^{-3}) and C (3694 m m^{-3}). The contribution of *S. megaphylla* to the combined root density of both species ranged from 39.7% in treatment A to 92.4% in treatment E.

Table 4.4. Mean root densities (m m^{-3}) of *P. patula* and *S. megaphylla* 32 months after establishment. Vertical lines link treatments not significant at the 5% level.

P. patula						*S. megaphylla*	
fine		coarse		total		total	
Contr.	718.9	Contr.	1394.5	Contr.	2113.4	E	8785
D	702.3	A	989.7	D	1648.8	D	6948
A	569.5	B	969.6	A	1559.2	C	3694
B	550.4	D	946.5	B	1540.0	B	2597
C	545.9	C	699.3	C	1245.2	A	1026
E	361.9	E	361.1	E	723.0	Contr.	0

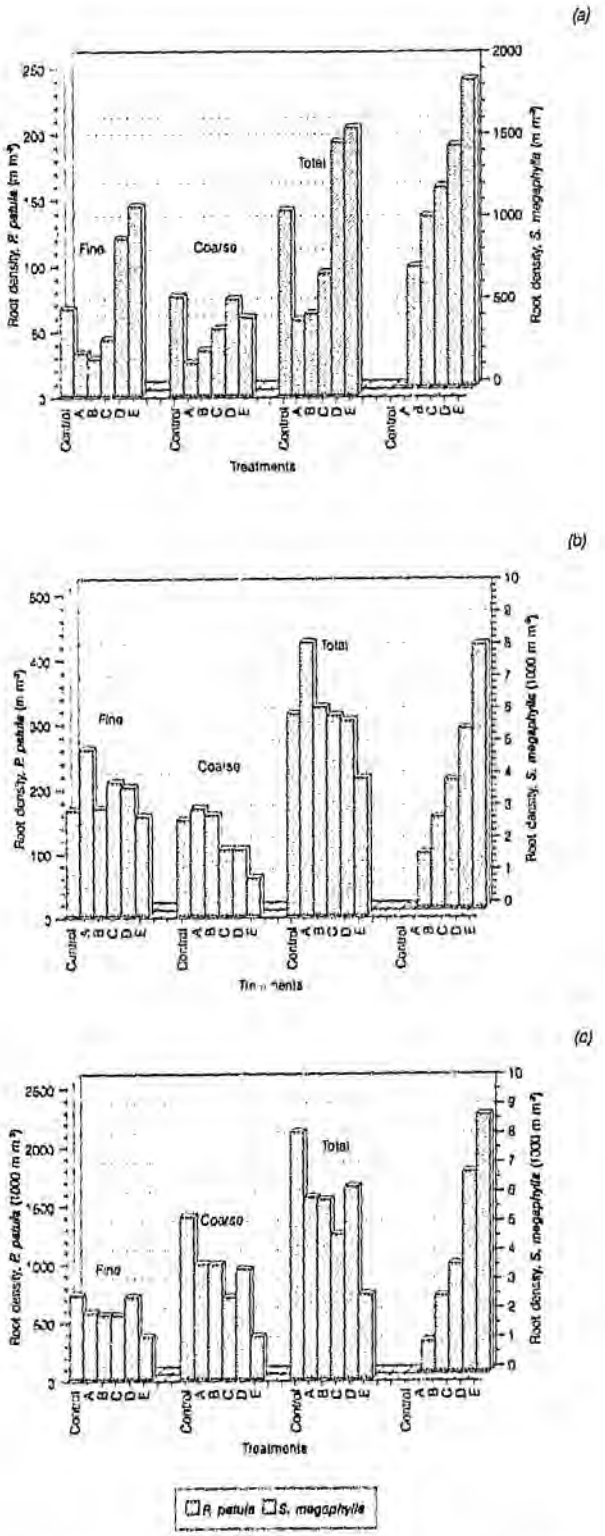


Figure 4.5. The root densities (m m^{-3}) of *P. patula* and *S. megaphylla* measured (a) 6, (b) 20 and (c) 32 months after establishment.

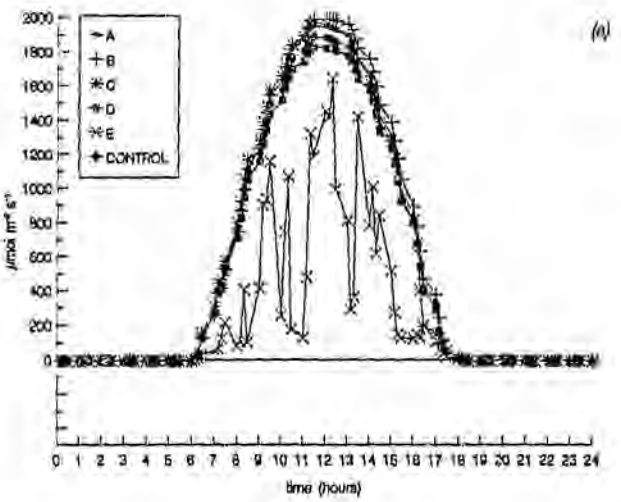


Figure 4.4. Diurnal photosynthetic active radiation (μmol m^{-2} s^{-1}) for the six competition regimes during March 1989.The length, mass and distribution of *P. patula* and *S. megaphylla* roots.

Root studies

Rooting densities for *P. patula* and *S. megaphylla*, 6, 20 and 32 months after planting are illustrated in Figure 4.5. Means and standard deviations of root densities for the various treatments are presented in Appendix 4. Six months after establishment the root densities for *P. patula* were low and ranged from 28 to 144 m m^{-3}. At this early stage, the rooting zone had not been fully occupied and no competitive interaction was observed. This is reflected in the response of the aboveground growth parameters for this period (Figure 4.1). The fine root density of *P. patula* in treatment E (144 m m^{-3}) was significantly greater than the densities of fine roots in the Control and treatments C, A and B. The fine root density of D (119 m m^{-3}) was significantly less than in treatment C, A and B. The greater fine root density of D and E could be ascribed to the moister conditions provided by the shading or mulching effect of the grass. Total root densities of *P. patula* (coarse and fine) followed similar trends to fine root densities. The contribution of fine roots to total root density ranged between 45 and 71%.

Six months after establishment, the root densities (figure 4.5a) of *S. megaphylla* clearly reflected the clipping regime, with treatment E having the greatest density (1865 m m^{-3}) and treatment A having the least (727 m m^{-3}). The total root densities of *P. patula* for the different treatments only contribute from 5.6 to 11.6% of the combined rooting density of both *P. patula* and *S. megaphylla*. A paired t-test comparing *P. patula* and *S. megaphylla* total root densities showed that differences between the two are

Table 4.7. Parameter estimates, coefficients of determination and standard errors for the linear relationship between $RGR_{P,leaf}$ and $RGR_{S,leaf}$.

Treatment	α	β	n	R^2	$SE_{coeff.}$	$SE_{Y\ est.}$
A	0.0016	1.125	27	0.84	0.098	0.0046
B	-0.0004	0.730	20	0.94	0.044	0.0027
C	0.00056	0.558	16	0.92	0.045	0.0019
D	0.000079	0.469	7	0.98	0.026	0.0009

Two questions arise. First, what is causing the differences in β between treatments, and second, how do these differences result in differences in productivity of *P. patula*? No relationships were found between the $RGR_{P,leaf}$ and $w_{S,leaf}$ at any particular time. It was therefore hypothesized that the differences are a result of either the frequency of clipping carried out for each treatment, or the mean mass of *S. megaphylla* that occurs for a particular treatment over the duration of the study period. The mean mass of *S. megaphylla* ($\overline{w}_{S,leaf}$) for a treatment is defined as

$$\overline{w}_{S,leaf} = \frac{\sum (w_{S,leaf}(t_2 - t_1)\ 0.5))}{t} \qquad (33)$$

where $w_{S,leaf}$ is the mass of *S. megaphylla* midway through an interval of t_2-t_1 days, and t the total length of time. The value $\overline{w}_{S,leaf}$ provides an approximation of how much *S. megaphylla* there is at any particular time for a specific treatment. The relationships between $RGR_{P,leaf}$ and $RGR_{S,leaf}$ for each treatment were harmonized in order to develop a singular function for all treatments. Functions of this nature are described by Plenaar (1965) and Plenaar and Turnbull (1973). Using the slope (β) as the dependent variable, the following relationship was developed

$$\beta = 1.576 - 0.198 \ln(\overline{w}_{S,leaf})$$

$$R^2 = 0.95$$

$$n = 4$$

Substituting for β in Equation 32 and assuming that the intercept (α) is zero results in the following function:

$$RGR_{P,leaf} = [1.58 - 0.198 \ln(\overline{w}_{S,leaf})]\ RGR_{S,leaf} \qquad (35)$$

Figures 4.18 a and b illustrate the $RGR_{P,leaf}$ and $RGR_{S,leaf}$ as functions of the mass of *P. patula*. The mass of *P. patula* is expressed logarithmically to illustrate treatment differences as it is difficult to graphically distinguish differences between treatments when $w_{P,leaf}$ is expressed linearly. For $RGR_{P,leaf}$, treatment differences are distinct. The highest $RGR_{P,leaf}$ occurred in the Control, and the lowest in treatment D. Although not as distinct, trends for $RGR_{S,leaf}$ can also be observed. These are the reverse of $RGR_{P,leaf}$, with the $RGR_{S,leaf}$ being lowest in treatment A and highest in treatment D.

Note that it is only in the early stages of growth that the $RGR_{P,leaf}$ for the different treatments varies. At this stage, the $RGR_{P,leaf}$ are highest in the Control and lowest in treatment D. These early differences may have important effects on the future growth of *P. patula*. Bradford and Hsaio (1982) discuss the time course of gross responses, and the fact that relatively small early differences in growth result in much larger differences than just proportional to the alteration. They consider this phenomenon as an example of positive feedback behaviour or amplification with time.

The $RGR_{S,leaf}$ also decreases with time albeit with a more irregular pattern. This most probably reflects seasonal effects and the effect of clippings. With the exception of the Control and treatment A, the $RGR_{S,leaf}$ for treatments B, C and D are higher than those for *P. patula*.

The $RGR_{P,leaf}$ as a function of $RGR_{S,leaf}$ for treatments A, B, C and D are illustrated in Figure 4.17.

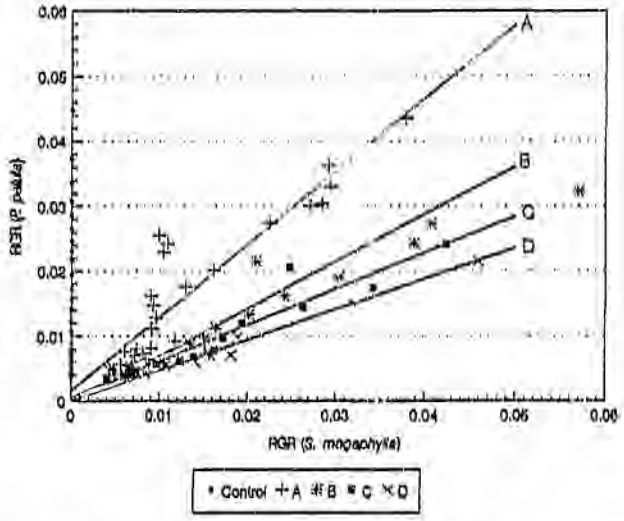


Figure 4.17. The relative growth rate of *P. patula* foliage as a function of the relative growth rate of *S. megaphylla* foliage.

There is a linear relationship between $RGR_{P,leaf}$ and $RGR_{S,leaf}$ for the various treatments which can be expressed by the function

$$RGR_{P,leaf} = \alpha + \beta RGR_{S,leaf} \qquad (32)$$

Parameter estimates, coefficients of determination and standard errors for the linear relationship between $RGR_{P,leaf}$ and $RGR_{S,leaf}$ for the various treatments are given in Table 4.8. The values for the slope (β), decrease with increasing competition, are highest in treatment A, and are lowest in treatment D.

4.1.4 The Interaction between *P. patula* and *S. megaphylla*.

Figure 4.16 shows the $RGR_{P,leaf}$ and $RGR_{S,leaf}$ for each treatment over time. The $RGR_{P,leaf}$ for all treatments display exponentially decreasing trends, levelling off at approximately 0.005.

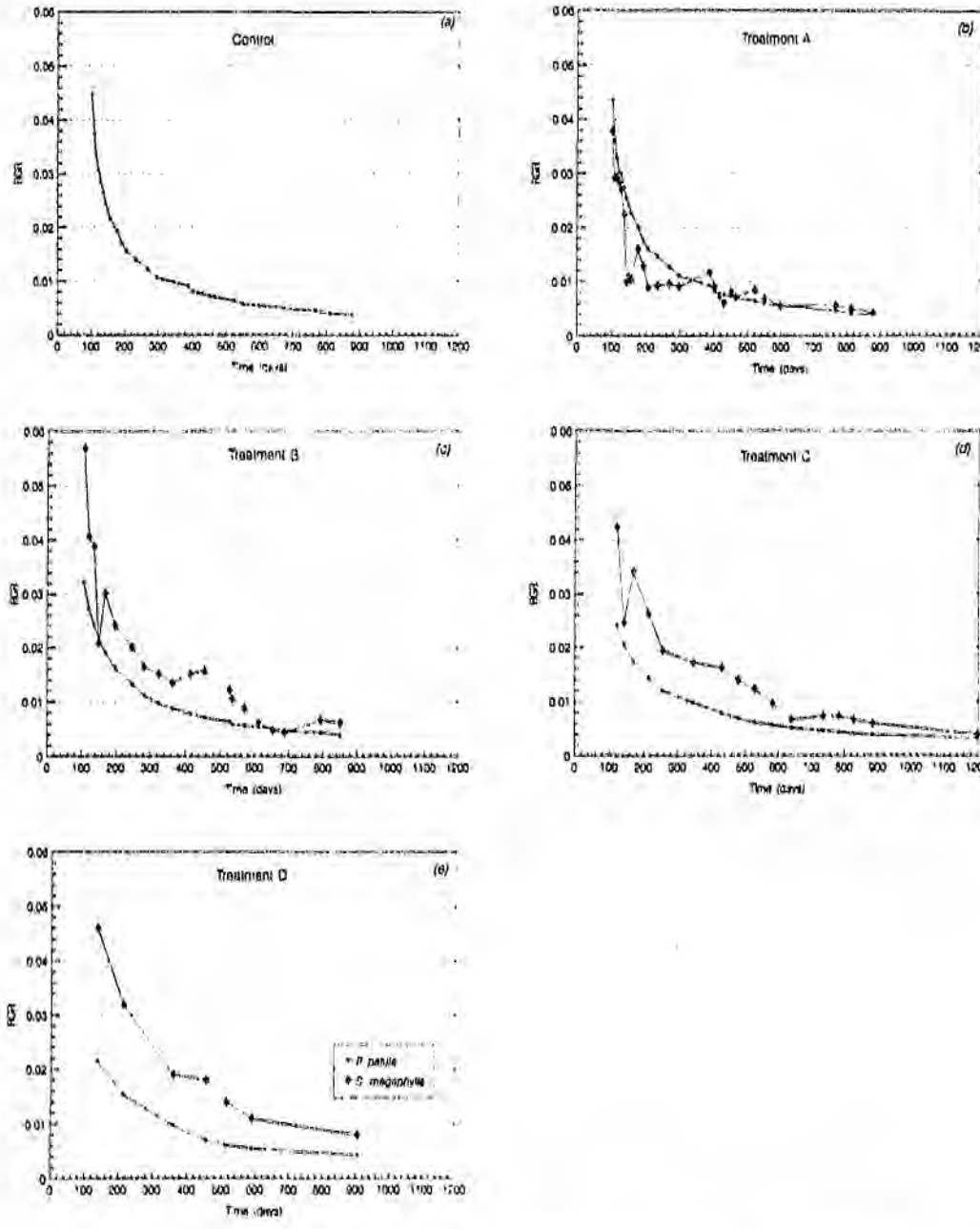


Figure 4.16. Relative growth rates for *P. patula* (▪) and *S. megaphylla* (♦) for the Control *(a)*, treatment A *(b)*, treatment B *(c)*, treatment C *(d)* and treatment D *(e)* as a function of time.

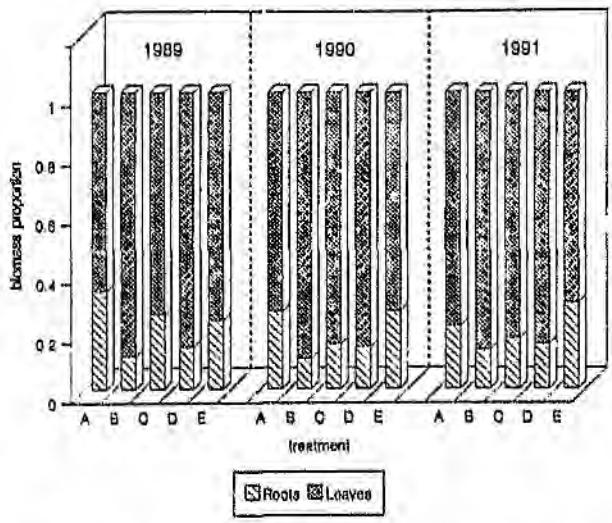


Figure 4.15. The proportions of root and leaf biomass in relation to total biomass for *S. megaphylla*.

$RGR_{W,grass}$ is highest in treatment D and lowest in treatment A. There is a strong inverse relationship between $RGR_{W,pine}$ and $RGR_{W,grass}$ for a specific treatment. Under high competition regimes, for example treatment D, the $RGR_{W,grass}$ is greater than the $RGR_{W,pine}$. Under low competition regimes, such as treatment A, the opposite holds true. The interaction between *P. patula* and *S. megaphylla* is discussed in more detail in the following section.

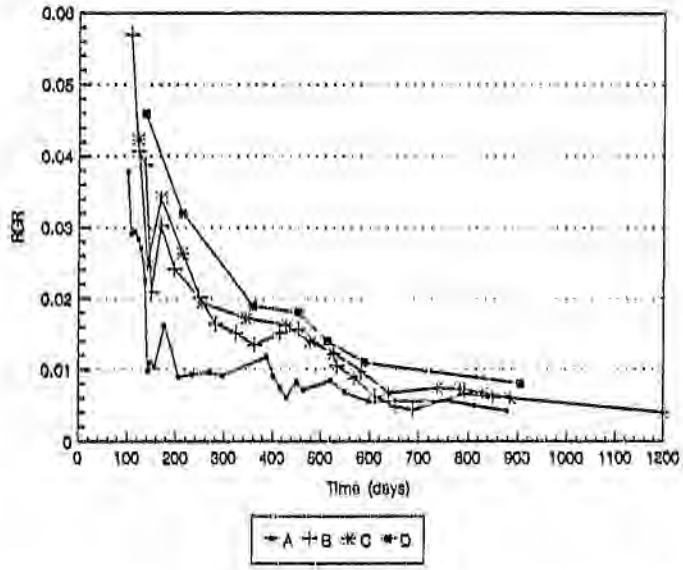


Figure 4.14. The relative growth rates ($RGR_{W,grass}$) for *S. megaphylla*.

Figure 4.15 shows η_{root} and η_{leaves} for *S. megaphylla* eight, 20 and 32 months after establishment. No clear trends for any of the sampling periods are apparent, although treatment B has the lowest η_{root} for all three sampling periods. After eight months, η_{root} ranges from 0.11 to 0.33. The highest η_{root} occurs in treatment A (0.33) and the lowest in treatment B (0.11). After 20 months treatment A and E have the highest η_{root} of 0.26. The lowest η_{root} occurred in treatment B (0.10). 32 months after establishment, the highest η_{root} occurred in treatment E (0.29) and the lowest in treatment B (0.13).

Figure 4.13 illustrates the cumulative aboveground biomass production of *S. megaphylla*. Treatment A, the lowest competition regime, has the lowest cumulative biomass of approximately 0.9 tons ha^{-1}. Treatments B and C have similar cumulative biomasses of approximately 5.0 and 5.3 tons ha^{-1} respectively . The similarity in the competitive effect of treatments B and C is reflected in the height, RCD and volume index (Figure 4.1) and biomass (Figure 4.10) of *P. patula*. The cumulative biomass of *S. megaphylla* in treatment D was 10 5 tons ha^{-1}, which was substantially higher than in treatments C and B. Subplots in treatment E were destructively sampled in January 1991 (5.7 tons ha^{-1}) and January 1993 (7.5 tons ha^{-1}) The relatively small change in biomass between the January 1991 and 1993 destructive sampling of treatment E suggests that, when the grass is not clipped, the maximum carrying capacity of the site is attained in a relatively short time, and is maintained at a fairly constant level. Of interest are the seasonal dips in the biomass accumulation rate for treatments B, C and D approximately 350 and 700 days after planting. The decrease in biomass accumulation rate coincides with winter, and could be due to a decrease in temperature or competition for water.

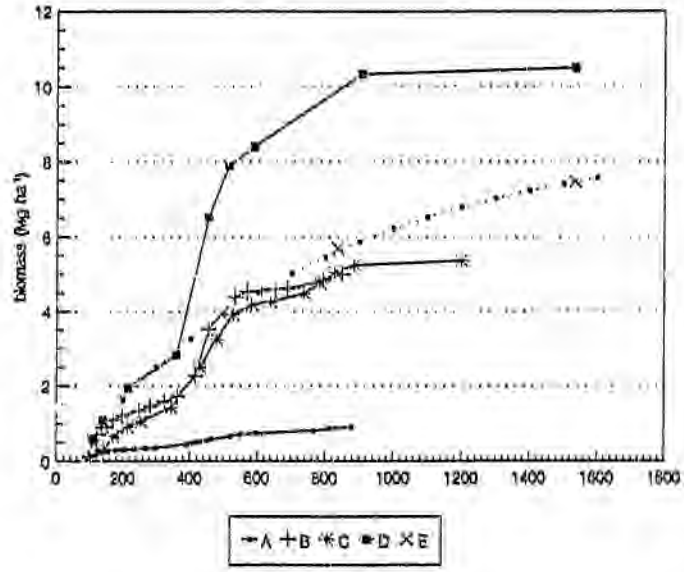


Figure 4.13. The cumulative aboveground biomass production of *S. megaphylla*.

The relative growth rates for the aboveground component of *S. megaphylla*, ($RGR_{W,grass}$), for the clipping sampling periods are illustrated in Figure 4.14. The $RGR_{W,grass}$ follows the same trend as *P. patula*, albeit in a more irregular manner. The $RGR_{W,grass}$ decreased at an exponential rate. Seasonal increases similar to those in $RGR_{W,pine}$ were observed. The more pronounced peaks in $RGR_{W,grass}$ suggest that *S. megaphylla* is more sensitive than *P. patula* to rainfall and temperature fluctuations. The maximum values for $RGR_{W,grass}$ range from 0.038 for treatment A (day 100) to 0.057 for treatment B (day 114). After approximately 750 days, the $RGR_{W,grass}$ values converge to between 0.004 and 0.008. Over time, the

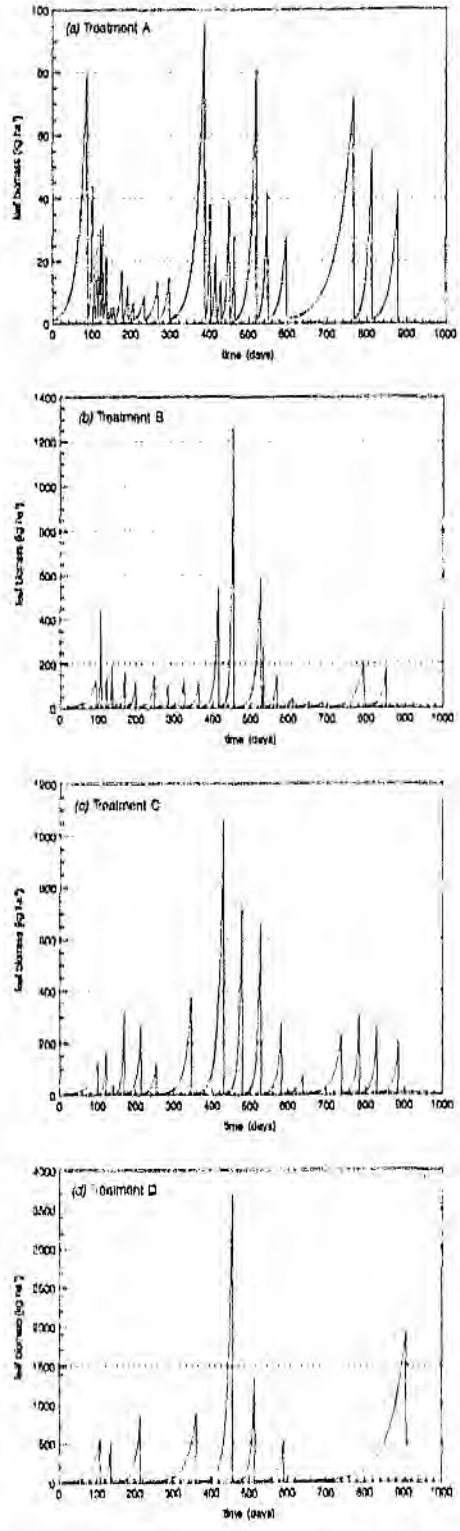


Figure 4.12. The clipping frequency and the mass harvested at each interval for (a) treatment A, (b) treatment B, (c) treatment C and (d) treatment D for *S. megaphylla*.

4.1.3 The biomass of *S. megaphylla*

Figure 4.12 illustrates the clipping frequency and the mass harvested at each interval for treatments A, B, C and D. Treatment A was clipped a total of 28 times, with the amount of leaves harvested ranging from approximately 5 to 95 kg ha^{-1}. Treatment B was clipped 21 times and the mass harvested ranged from 20 to 1260 kg ha^{-1}. Treatment C was harvested 16 times and the amount harvested ranged from approximately 30 kg ha^{-1} to over 1050 kg ha^{-1}. Although the frequency of harvesting in treatment C is lower than in treatment B, the amount harvested did not differ markedly. From this it can be surmised that the competitive impact of *S. megaphylla* in treatments B and C on the growth of *P. patula* is similar. Treatment D was harvested eight times and the mass of clippings ranged from approximately 50 to 3700 kg ha^{-1}.

No clippings took place in Treatment E. The amount of aboveground biomass was determined from harvests in the destructive sampling zone. Using the destructive samples, the biomass of *S. megaphylla* in treatment E was estimated using the equation:

$$W_E = a\left[1-(b\exp^{(-ct)})\right] \qquad (31)$$

where a = 8495.0 ± 1281.4,
b = 1.094 ± 0.089,
c = 0.0014 ± 0.0006, and
t = time (days)

Unfortunately, the frequency of destructive sampling of *S. megaphylla* in treatment E was too low (three times for each replication). Therefore, temporal or seasonal fluctuations in the aboveground biomass could not be accurately determined.

establishment, trees growing under the lowest competition regimes had attained canopy closure thereby suppressing the growth of *S. megaphylla*. It is hypothesized that at this stage, with the exception of treatment E, a transition from interspecific to intraspecific competition had occurred. As trees, were now competing with each other, especially in the Control and treatment A, more assimilates were allocated to root growth. Treatment E had the highest RGR_d and could have been under less 'competitive stress'. Therefore, in treatment E, less assimilates were allocated to the roots. The η_{stem} for all treatment increased from the July 1990 evaluation. The η_{stem} was greatest in treatment E (0.34), and lowest in treatment B (0.16). The η_{branch} for the July 1991 evaluation period also increased. The η_{branch} was greatest in treatment B (0.33), and lowest in treatment E (0.14). The η_{needle} did not alter noticeably from July 1990 to July 1991, although the proportion of assimilate allocated to treatment E, which was the lowest in 1990, was the highest in 1991.

Increases in root growth relative to shoot growth have been shown by numerous authors (e.g. Bradford and Hsalo (1982), Jones (1983), McMurtrie and Wolf (1983a), Landsberg (1986), Axelsson and Axelsson (1986) and McMurtrie and Landsberg (1992)). Bradford and Hsalo (1982) are of the opinion that differences in allocation can be attributed mostly to decreases in shoot growth, although there are instances where water stress has caused an increase in absolute root mass. Axelsson and Axelsson (1986), studying changes in carbon allocation in *P. sylvestris*, found that in a water stress experiment, drought would increase root growth relative to shoot growth. They concluded that root/shoot partitioning might be a major determinant of growth rate capacity in seedlings and young trees, and that different carbon allocation strategies may be the key mechanism in interspecific competition.

This study illustrates the dynamics of carbon allocation in young stands, and how carbon allocation changes with age and different levels of competition. It also illustrates the importance in including the belowground biomass component in order to avoid misinterpretation.

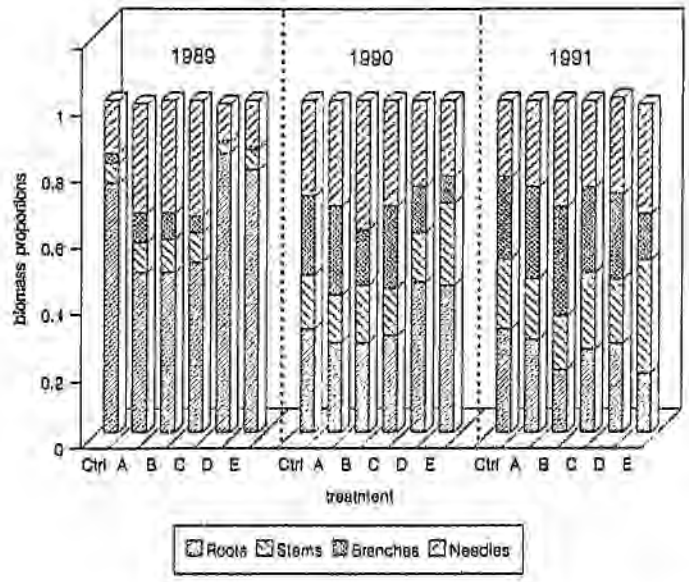


Figure 4.11. The proportions of root, stem, branch and needle biomass in relation to total biomass of *P. patula*.

In July 1990, the η_{root} declined by approximately 50%. At this measurement period, the greatest η_{root} occurred in treatments D and E, those species growing under the highest competition regimes. It is hypothesized that the trees growing under adverse conditions are allocating more assimilate to root growth in order to 'colonize' a greater proportion of the soil.

The η_{stem} was greatest in treatment E (0.25) and lowest in treatments A and C (0.14). The η_{branch} was greatest in treatments C (0.25) and A (0.24) and lowest in treatment E (0.08). The amount of assimilate allocated to aboveground structural mass (stems and branches) is greatest for Treatment A and the Control, and lowest in treatment D and E. The η_{needle} was greatest in treatment B (0.39) and lowest in treatment E (0.23).

The period between June 1989 and July 1990 showed the greatest variances in RGR_d, RGR_n and RGR_w between the different treatments (Figure 4.3). We can assume that interspecific competition at this stage was the most vigorous. The proportion of assimilates allocated to each of the biomass components reflects the competitive strategy of *P. patula* for this period, which was to allocate a greater proportion of carbon assimilates to the roots of trees growing under the higher competition regimes.

In July 1991, the η_{root} decreased relative to the other biomass components. The η_{root} was greatest in the Control (0.31) and treatment A (0.28), and lowest in treatment E (0.18). Approximately 985 days after

the Control to 0.41 in treatment E. The η_{branch} was similar to that of July 1990, with treatment E still having the lowest η_{branch} (0.17). The η_{stem} for all treatments remained unchanged for all three sampling periods, with treatment E consistently having the greatest η_{stem}.

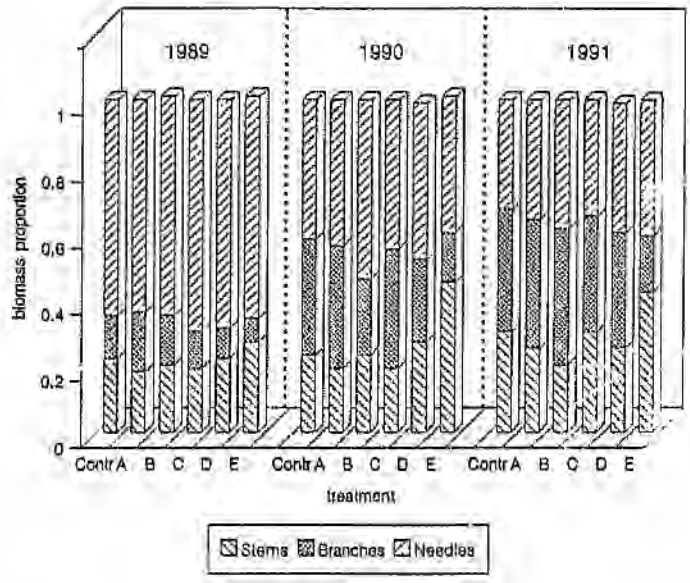


Figure 4.10. The proportions of stem, branch and needle biomass in relation to aboveground biomass of *P. patula*.

The proportions of stem, branch and needle biomass (aboveground biomass components) were compared to the proportions of root, stem, branch and needle biomass (total biomass components). Figure 4.11 shows η_{root}, η_{stem}, η_{branch} and η_{needle} in relation to total biomass for *P. patula* eight, 20 and 32 months after establishment. The sample sizes, means and standard deviations are presented in Appendix 8. The least squares means and probability va[illegible] presented in Appendix 9. In June 1989, 8 months after establishment, the η_{root} was the greates[illegible] treatments. It is theorized that at this stage all treatments are allocating assimilate to root growth in order to maximize occupation of the site. The η_{root} ranged from 0.84 in treatment E to 0.48 in treatments A and B. The second greatest amount of assimilate was allocated to needles and η_{needle} was 0.11 in treatment D and 0.35 in treatment C. There was a strong relationship between the η_{needle} and η_{branch}. The greater the η_{needle} the greater the η_{branch} indicating allocation of more assimilate to branches so as to support a larger canopy. The smallest amount of assimilate was allocated to branches in treatments D and E, which correspondingly had the smallest η_{needle}. The η_{stem} ranged from 0.03 in treatment D to 0.10 in treatment B.

The relative growth rates with respect to needle mass, ($RGR_{W,pine}$), corresponding to the measurement intervals over approximately three years are shown in Figure 4.9. Trends in $RGR_{W,pine}$ were generally the same as for RGR_d, RGR_h and RGR_{vl}. There was an initially high RGR, followed by an exponential decline, with slight increases in $RGR_{W,pine}$ corresponding with increased rainfall periods. The RGR_{Wpine} reflects the competition regimes up to the day 601 interval. The variances in $RGR_{W,pine}$ between the treatmen decreases after this interval, at which stage the $RGR_{W,pine}$ for treatment E becomes the highest.

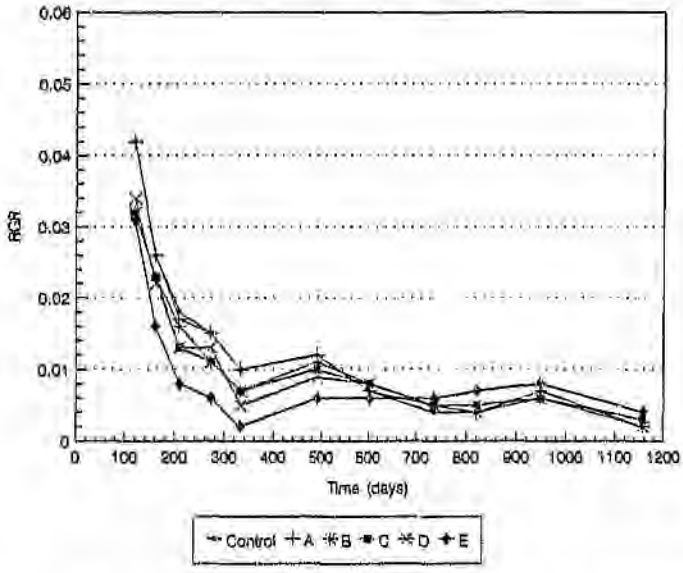


Figure 4.9. The relative growth rate (RGR_W) of *P. patula* at measurement intervals over a period of approximately three years.

Figure 4.10 presents η_{stem}, η_{branch} and η_{needle} in relation to aboveground biomass for *P. patula* eight, 20 and 32 months after establishment. The sample sizes, means and stan deviations are presented in Appendix 6. The least squares means and probability values are presented in Appendix 7. In June 1989, η_{stem} ranged from 0.18 (treatment A) to 0.27 (treatment E). For the same period η_{needle} ranged from 0.64 for treatment A to 0.70 for treatment C. The smallest amount of assimilate was allocated to branches. No marked differences in biomass allocation at this interval could be observed, except that for treatment E, where, in relation to the other treatments, the proportion of branch biomass was lowest and stem biomass highest.

In July 1990, the η_{needle} decreased and η_{branch} increased for all treatments. The η_{needle} ranged from 0.41 in treatment E to 0.54 in treatment B. The η_{branch} was lowest in treatment E (0.15) and greatest in treatment A (0.37). In general, the η_{stem} for all treatments except treatment E remained unchanged. The η_{stem} for treatment E increased to 0.45. In July 1991 the η_{needle} decreased further to range from 0.33 in

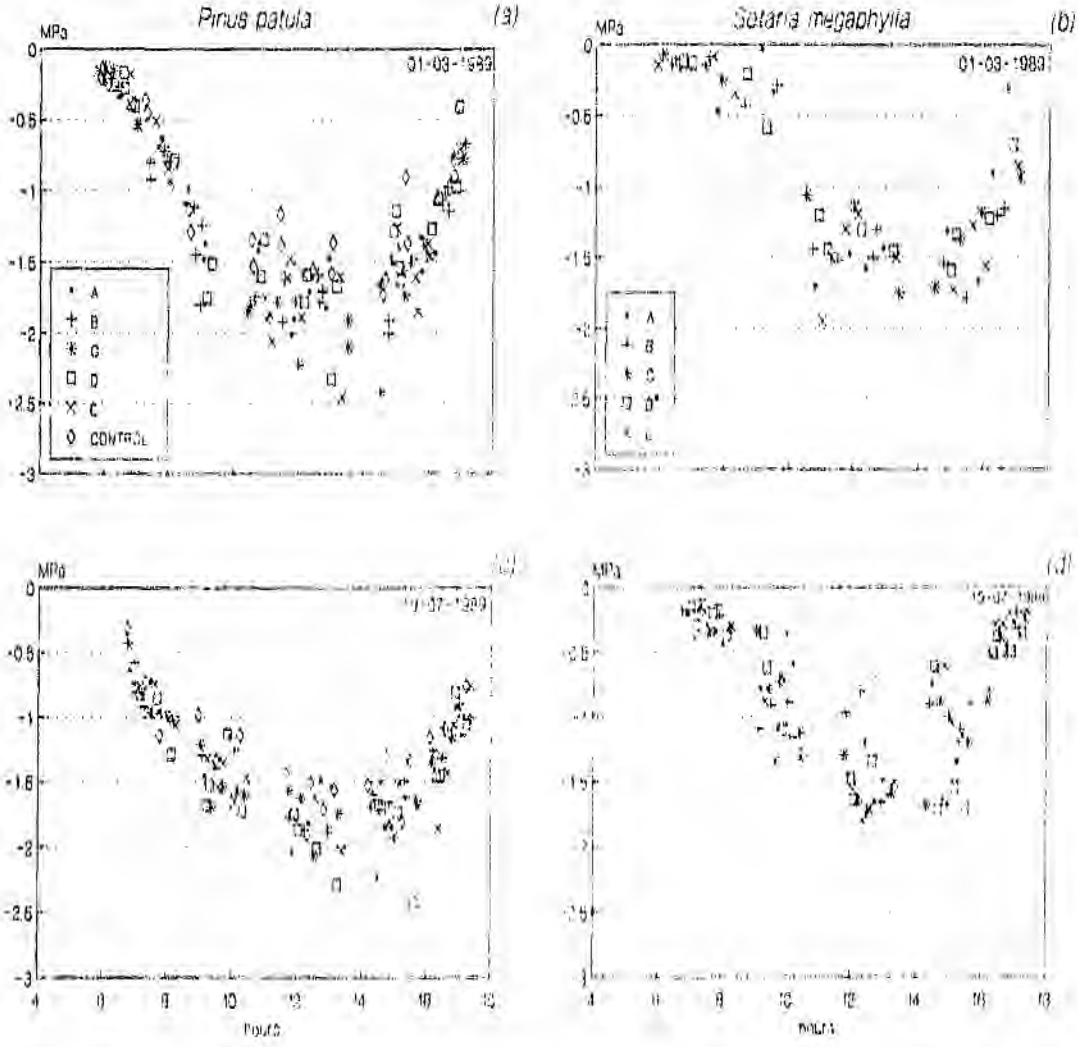


Figure 4.27. Diurnal water potential trends for (a) *P. patula* in March 1989, (b) *S. megaphylla* in March 1989, (c) *P. patula* in July 1989 and (d) *S. megaphylla* in July 1989.

Figure 4.27 shows the diurnal water potential trends for *P. patula* and *S. megaphylla* in March and July. Although clear diurnal trends were observable, no conclusive distinctions between the different competition regimes could be made. The lowest water potentials occurred between 12h00 and 15h00. The lowest water potentials for *P. patula* lay between -2.0 and -2.5 MPa. Water potentials for *S. megaphylla* were less negative and lay between -1.5 and -2.0 MPa. In July, recovery rates to water

negative than the other treatments. Pre-dawn ψ_{pine} for treatments A, B and Control continued to decrease over time. However, the pre-dawn ψ_{pine} of treatments C and D increased by 0.1 and 0.08 MPa respectively, and were not significantly different to treatments A, B and the Control. The reason for these increases was not readily apparent and could be due to erroneous readings on under-developed needles.

There is strong evidence to suggest that, in many field situations, competition for water is the most limiting factor in the early growth of *P. patula*. The most obvious effect of even a mild stress is to reduce growth . Cell expansion is particularly sensitive to water deficits, with the rate of cell expansion of several species being slowed by any reduction in ψ below -0.2 MPa. Cell expansion is completely inhibited by ψ between -0.4 and -1.2 MPa (Bradford and Hsaio 1982). The ψ of trees rarely falls below -2.0 MPa, irrespective of tree size or the amount of canopy (Richter 1976; Waring and Schlesinger 1985). Cell division is less sensitive to water stress than cell expansion (Bradford and Hsaio 1982). The turgor pressure in the growing cells provides the driving force for cell expansion. The expansion rate depends more on turgor pressure than total water potential. There is evidence that the rate of expansion is proportional to the excess ψ over a certain threshold value (Jones 1983).

Rook *et al.* (1977) found that stem diameter and root growth in *P. radiata* were reduced by soil water deficit before transpiration and photosynthesis were affected. Sands and Correll (1976) found that the elongation rate of needles of *P. radiata* seedlings was closely related to the water potential of the rooting medium, even when the w er potentials were quite high. The relative growth rates of *P. patula*, as reflected by root collar diameter, height and volume index, were closely related to plant water potential. At approximately 210 days after planting, when differences in the relative growth rates for the various competition regimes became clearly evident (Figure 4.3a, b and c), the water potentials for *P. patula* began to decrease.

The pre-dawn ψ_{grass} for *S. megaphylla* were less negative than for *P. patula*, although they followed the same trends. A rapid drop in ψ_{grass} for all treatments occurred in May and by July, differences were significant ($F_{5,32} = 5.40^{**}$). In September, treatments A and B had the least negative water potentials of -0.33 and -0.28 MPa respectively. Trentment E, with a ψ_{grass} of -0.82 MPa, was significantly more negative than the other treatments. Intraspecific competition in treatment E was the main contributor to negative *S. megaphylla* water potentials.

4.3.3 Plant water potential

The differences in θ_v were manifested in pre-dawn plant water potential readings (Figure 4.26), which for *P. patula* and *S. megaphylla* dropped rapidly from May onwards, approximately 210 days after planting (Figure 4.26). The means, standard deviation, standard error and sample size for pre-dawn ψ_{pine} and ψ_{grass} are presented in Appendices 10 and 11.

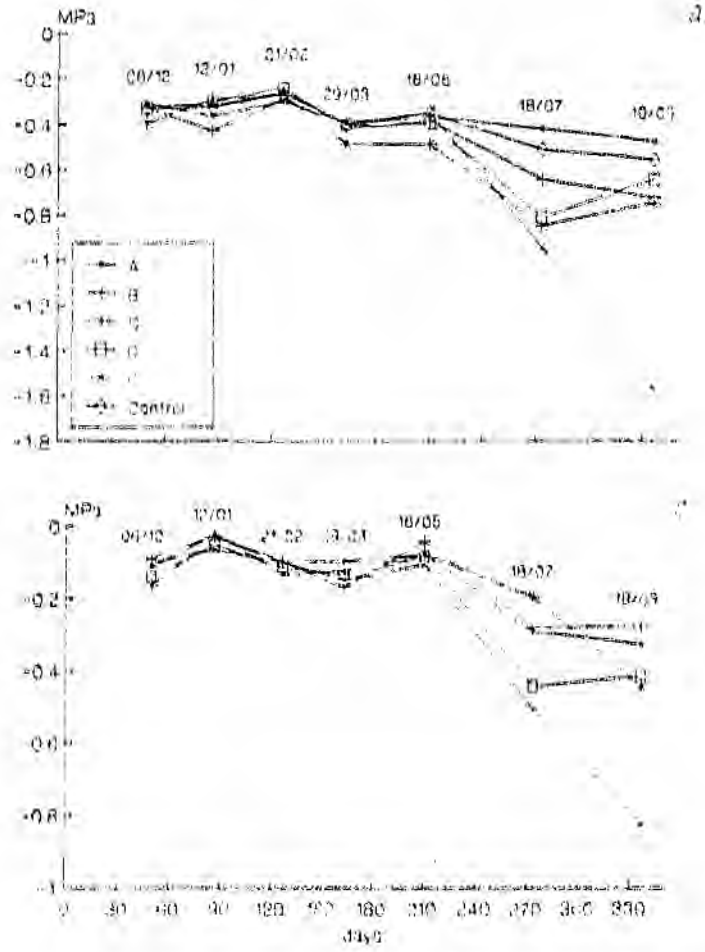


Figure 4.26. Pre-dawn plant water potential for *(a) P. patula* and *(b) S. megaphylla*.

By July, 272 days after planting, overall differences in ψ_{pine} for *P. patula* were significant ($F_{5,93} = 5.97^{***}$) Treatments A, B and Control were not significantly different from each other and were the least stressed. The ψ_{pine} of these treatments were significantly less negative than treatment E. In September, 336 days after planting, treatment E was the most stressed with a value of -1.6 MPa. This was significantly more

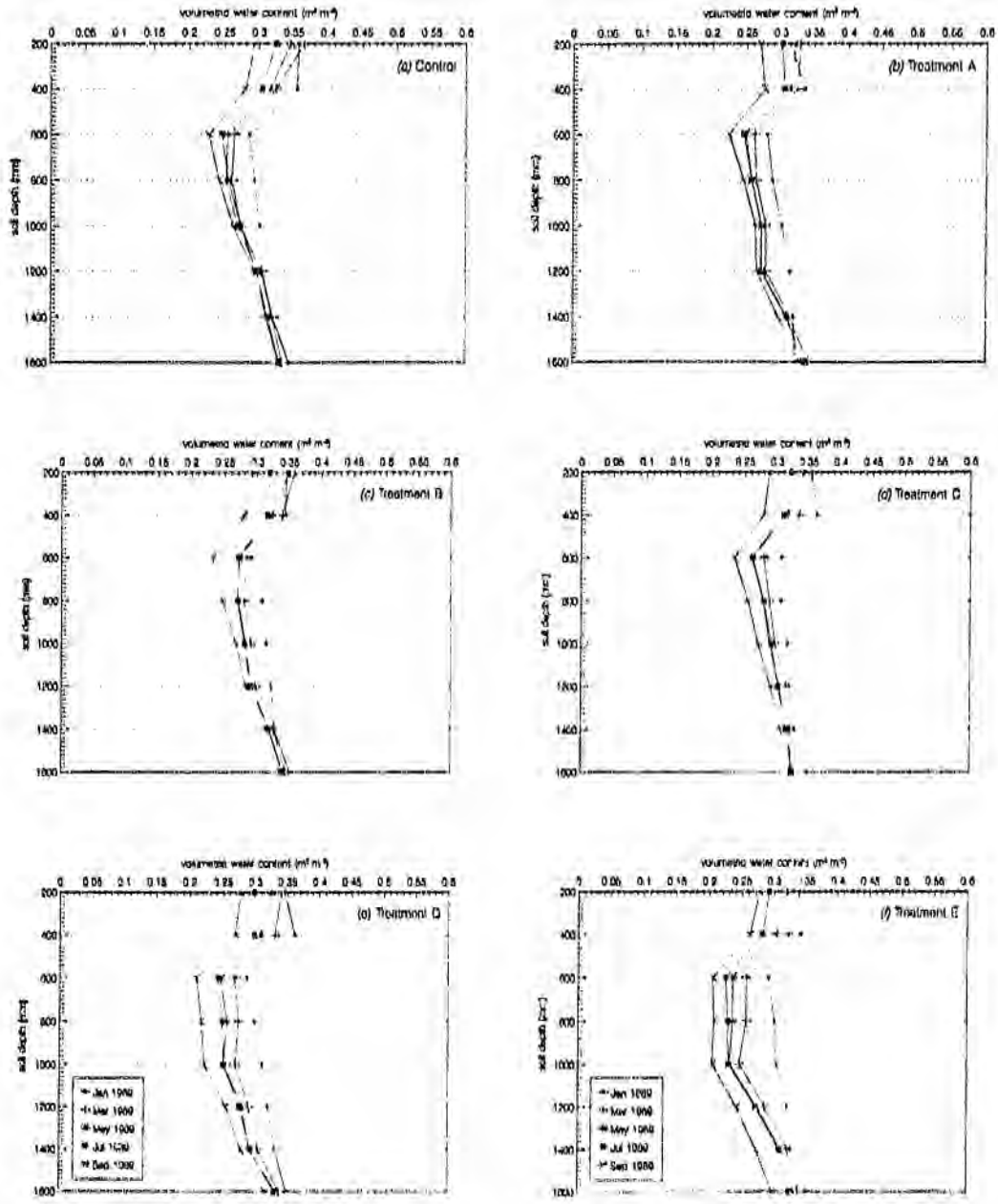


Figure 4.25. The volumetric soil water content, θ_v, for the different treatments and depths measured at two-monthly intervals.

regimes. Therefore, *S. megaphylla* under the high competition regimes causes a drying out of the soil profile. This is due to the higher densities of roots in the lower depths in the soil profile.

At the depth of 200 mm, treatments A and E had the lowest θ_v during September 1989, approximatel y 320 days after establishment. At this time θ_v for treatments A and E were 0.27 and 0.28 $m^3 m^{-3}$ respectively. The highest θ_v at this time was in treatment B (0.29 $m^3 m^{-3}$), which is only 0.02 $m^3 m^{-3}$ greater than that of treatment A. This narrow range in θ_v between treatments at this depth continued for the duration of the trial.

At a depth of 400 mm, lower θ_v values of 0.30 and 0.28 $m^3 m^{-3}$ were recorded in July, approximately 280 days after establishment in treatments D and E respectively. The lowest θ_v values for this depth were recorded in September 1989, and ranged from 0.28 $m^3 m^{-3}$ in treatment A to 0.26 $m^3 m^{-3}$ in treatment E, a difference of 0.02 $m^3 m^{-3}$. As with the 200 mm depth interval, , in all treatments varied little between each other over time.

At the 1000 mm depth, lower θ_v values were observed in treatments D and E in February 1989, approximately 130 days after establishment. In September 1989, the θ_v of the treatments clearly reflected the competition regimes. The highest values were recorded in the Control (0.26 $m^3 m^{-3}$) and lowest values in treatment D (0.22 $m^3 m^{-3}$) and treatment E (0.20 $m^3 m^{-3}$).

The θ_v at eight depths in the soil profile, and measured at two-monthly intervals from January to September 1989, are shown in Figure 4.25. This period was chosen as, based on relative growth rates, it was believed to be the critical period with respect to competitive interactions.

Patterns of θ_v at different depths were remarkably consistent. In all treatments and at all depths, a decrease in θ_v occurred with time. The last measurements plotted in Figure 4.25 were taken in September 1989, at the end of winter. An increase in the θ_v in the profiles could be expected with the onset of the spring rains. For individual treatments at specific times, there was little difference in θ_v between the 200 and 400 mm depths. The θ_v decreased from the 400 to 600 mm depth, followed by a gradual increase in θ_v up to a depth of 1600 mm. Differences in the θ_v at these depths for different times increased with increasing levels of competition. For example, in the Control, at a depth of 1.0 m, the difference in θ_v between the January and September readings was only 0.01 $m^3 m^{-3}$. In treatment E, for the same depth and period, the difference in θ_v was 0.08 $m^3 m^{-3}$. The absolute values of θ_v at this depth were highest in the Control (0.29 $m^3 m^{-3}$) and lowest in treatment E (0.24 $m^3 m^{-3}$).

These differences in θ_v appear to be related to the rooting density of *S. megaphylla* (Figure 4.7a). During this period most of the *P. patula* roots occupy the top 300 mm of the soil profile. The amount of *P. patula* roots decreases rapidly with increasing levels of competition. On the other hand, *S. megaphylla* roots occupy the whole of the soil profile, more so at the higher competition

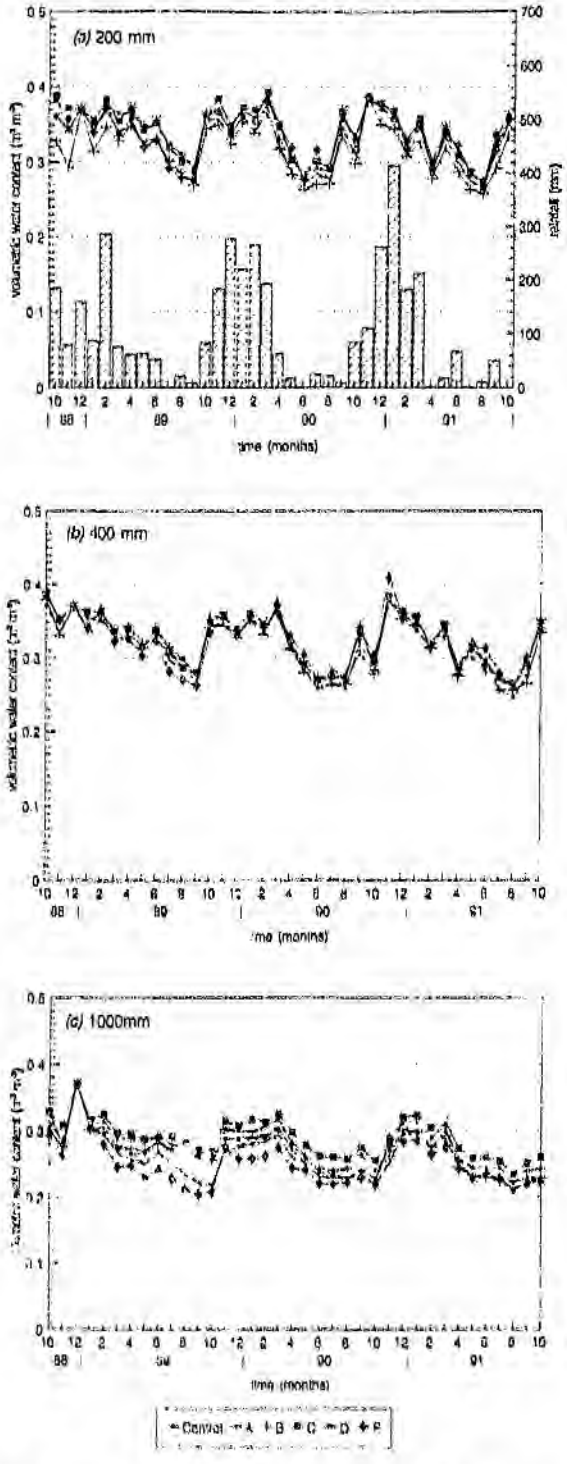


Figure 4.24. The volumetric soil water content, ϑ_s, for the different treatments at depths of (a) 200, (b) 400 and (c) 1000 mm for the period October 1988 to October 1991.

4.3 Competition for water

4.3.1 Rainfall

Figure 4.23 illustrates monthly rainfall for the first three years of the study. Three distinct peaks occurred in February 1989 (257 mm), December 1989 (276 mm) and January 1991 (414 mm). During 1989, 1990 and 1991, the driest months were from June to August. In comparison to the long-term rainfall records, monthly rainfall for the period October 1988 until June 1989 was approximately 206 mm below the long-term mean. For the periods July 1989 until June 1990, and July 1990 until June 1991, the rainfall was approximately 74 and 144 mm above the long-term mean of 1250 mm.

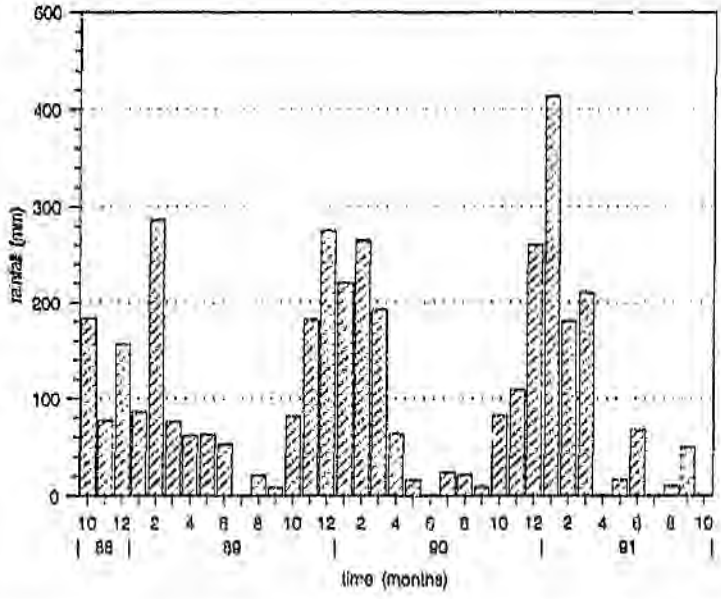


Figure 4.23. Monthly rainfall, (mm), for the period October 1988 to October 1991.

4.3.2 Soil water

Figure 4.24 illustrates soil water content (θ_s) at depths of 200, 400 and 1000 mm in the soil profile for the six different competition regimes. Note how closely soil moisture trends followed rainfall events. This was especially evident at the depth of 200 mm, while responses were more buffered at 400 and 1000 mm. Initially, the θ_s at all three depths decreased from December 1988 until September 1989. The increase in soil moisture during October 1989 corresponded to an increase in the monthly rainfall and this correlation with rainfall continued throughout the duration of the trial.

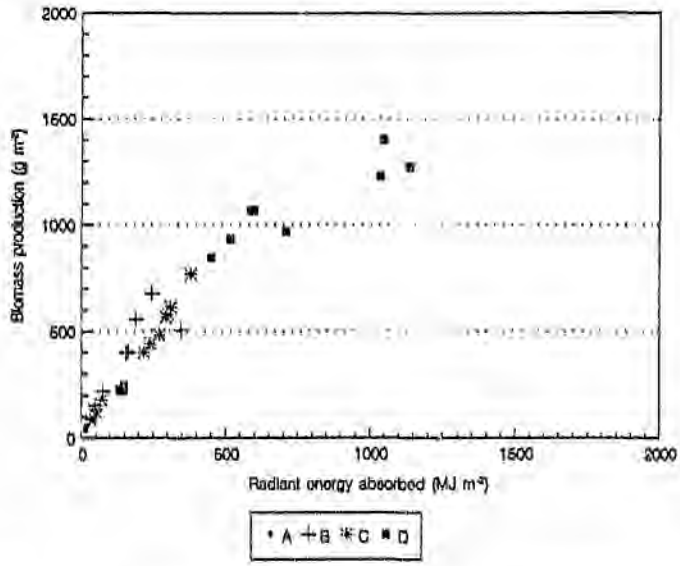


Figure 4.22. Cumulative total biomass production of *S. megaphylla* as a function of radiant energy absorbed.

In conclusion, the values for ε for *P. patula* appear to be limited by water and/or nutritional stress. Over short periods, the effects of water stress would be physiological, causing stomatal closure. Over longer periods water stress would cause a reduction in cell division and expansion leading to a decrease in the leaf area and hence $\varphi_{s,abs}$. Reduction in productivity is proportional to the water stress integral (Myers 1988), and will be examined in the following section. Nutritional stress could reduce the quantity of the carbon assimilation enzyme, ribulose bisphospate carboxylase (Bidwell 1974, Long and Hällgren 1993), which in turn would affect the rate of photosynthesis and consequently the value of ε. Landsberg (1995) cites examples where high leaf N concentrations increase the radiation use efficiency of crops. There is also evidence to suggest that N fertilisation increases ε in plantations (Raison and Myers 1992). Changes in the dynamics of the leaves (e.g., phyllotaxis, leaf initiation, senescence and shedding) could also occur.

carbon content of plant tissues (Brown and Lugo 1982, Harmon *et al.* 1990), aboveground ϵ values for *P. radiata* ranged from 1.14 to 1.34 g MJ^{-1} (Ralson and Myers 1992). *P. radiata* growing under conditions of water stress had aboveground ϵ values of 0.72 g MJ^{-1} (Myers and Talsma 1992).

Table 4.8. Estimates of the light-use efficiencies of *P. patula* growing under different competition regimes.

Treatment	ϵ (g MJ^{-1})	R^2	SE of coeff.
Control	0.82	0.99	0.029
A	0.85	0.99	0.029
B	0.59	0.99	0.012
C	0.68	0.97	0.036
D	0.58	0.99	0.018
E	0.36	0.98	0.016

If one assumes that the trees growing in treatment A or the Control are suffering no serious growth restrictions, and that the slopes of the upper two lines can be taken to define the highest efficiency in terms of radiant-energy conversion and biomass production, then all remaining treatments whose lines fall below that of treatment A and the Control are less productive. These differences in productivity may have been caused not only by differences in leaf production, but also by differences in energy conversion efficiency. Figure 4.21 shows that, for a given amount of radiant energy absorbed by the needles of a particular treatment, productivity varies with the level of competition. The results show clearly that the efficiency of light-use is reduced as a result of water or nutritional stress. Also that radiant energy (light) itself is not limiting the growth of *P. patula*. In theory, if light was limiting the growth of *P. patula* under different competition regimes, for a given time, values for ϵ for all treatments would fall upon the same line, but tend closer to zero as the level of light competition increased.

The relationship, between biomass production and radiant energy absorbed for *S. megaphylla* for treatments A, B, C, and D is illustrated in Figure 4.22. The values for ϵ are higher than those for *P. patula*, and range from 1.15 g MJ^{-1} in treatment D to 2.68 g MJ^{-1} in treatment B. No trends in the values of ϵ with respect to competition regimes was observed. The light-use efficiency values fall within the range cited by Cannell *et al.* 1987 for non-woody plants. From Figure 4.22, it can be clearly seen that the greatest cumulative production occurred in treatment D, followed by treatment B and C, and then treatment A. Compared to *P. patula*, for a certain amount of radiant energy absorbed by *S. megaphylla*, there is less differentiation in biomass production between treatments. The decrease in the cumulative biomass production is primarily determined by the frequency of clippings. This frequency obviously determines the amount of leaf area present in a certain treatment at a given time, and consequently $\varphi_{s.area}$.

4.2 The light-use efficiency of *P. patula* and *S. megaphylla*

The relationship between biomass production and radiant energy absorbed for *P. patula* is illustrated in Figure 4.21. The differences in the slopes indicate differences in the energy-conversion efficiency, ε. There is an inverse relationship between the level of competition and ε. Treatment A and the Control which had little or no restriction on growth from *S. megaphylla*, have the highest growth efficiencies of 0.85 and 0.82 g MJ^{-1} respectively. Their energy conversion efficiency is reflected by the upper two lines. The lowest line reflects the growth efficiency of trees growing in treatment E, the highest competition regime. Treatment E has a light use efficiency of 0.35 g MJ^{-1}, less than half that of treatment A and the Control.

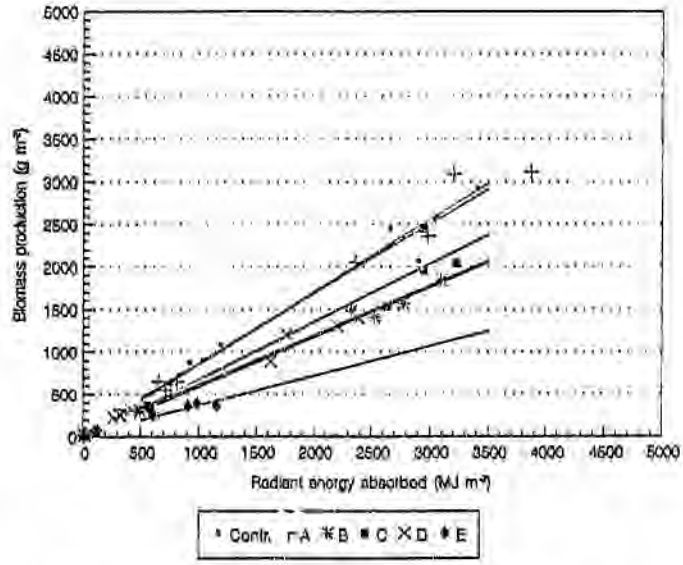


Figure 4.21. Total biomass production of *P. patula* as a function of radiant energy absorbed.

Estimates of ε for all treatments are shown in Table 4.8. Values fall within the ranges for woody species cited by a number of authors. Most studies on the relationship between biomass production and absorbed radiant energy have used aboveground components. Cannell *et al.* (1987) cites aboveground values of 0.5 g MJ^{-1} for *Eucalyptus globulus*, 0.7-0.9 g MJ^{-1} for *P. sylvestris*, and 1.6 g MJ^{-1} for irrigated and fertilised *P. sylvestris*. Cannell *et al.* (1988) recorded total values of 1.58 and 1.5 g MJ^{-1} for *Salix* and *Populus* clones respectively. Landsberg and Wright (1989) working on *Populus* clones in the United States, recorded aboveground values of 0.32 g MJ^{-1} and 1.4 g MJ^{-1} in the second year. A number of authors cite ε in terms of carbon content. Assuming a conversion factor of 50% to estimate the organic

The simulated values of $RGR_{P,leaf}$ for treatments A, B, C, and D as a function of their actual values are shown in Figure 4.20.

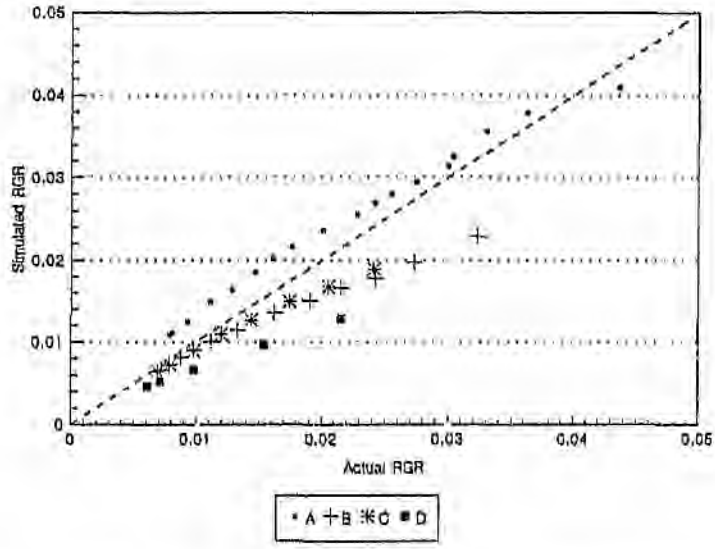


Figure 4.20. The simulated values of $RGR_{P,leaf}$ as a function of the actual values of $RGR_{P,leaf}$ for treatments A, B, C, and D. The dotted line represents a 1:1 relationship between actual $RGR_{P,leaf}$ and simulated $RGR_{P,leaf}$.

Figure 4.20 indicates that the simulated values for treatment A are slightly overestimated. However, the most that $RGR_{P,leaf}$ is overestimated in treatment A is by 0.003. Simulated $RGR_{P,leaf}$ values for treatments B, C and D are underestimated. The greatest underestimation occurs in treatment D. It is recognized that if a better function describing the relationship between $RGR_{S,leaf}$ and $w_{P,leaf}$ is developed, the degree of over and under estimation would be reduced.

The objective of this study was to determine which variables had a significant impact on foliage production of *P. patula*. We can conclude that both the $RGR_{S,leaf}$ and $\bar{w}_{S,leaf}$ were the most important variables used to determine $RGR_{P,leaf}$ and consequently $w_{P,leaf}$. With the knowledge of $w_{P,leaf}$, η_{root}, η_{stem}, η_{branch} and η_{needle} it is possible to determine the mass of each biomass component.

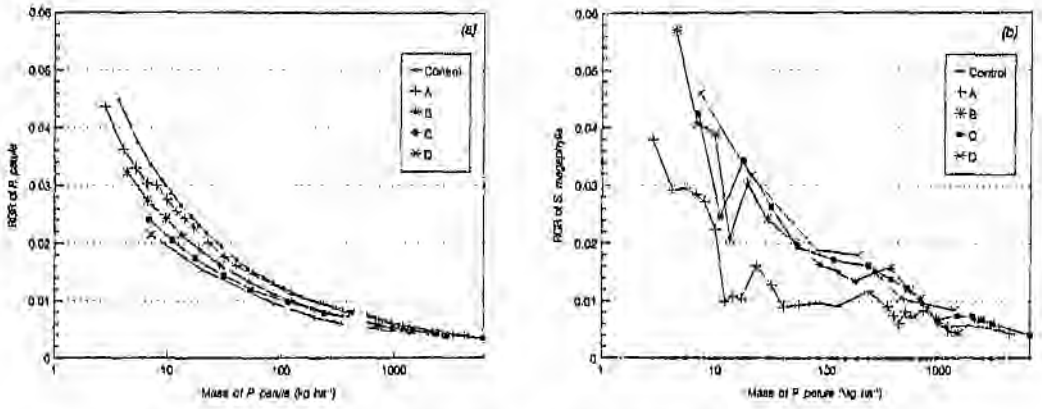


Figure 4.18. The relative growth rates of *P. patula (a)* and *S. megaphylla (b)* as a function of the mass of *P. patula*. Mass of *P. patula* is expressed on a logarithmic scale.

The relationship between $RGR_{S,leaf}$ and $w_{P,leaf}$ can be expressed as:

$$RGR_{S,leaf} = \exp(-3.006 - (0.273 \ln(w_{P,leaf}))) \quad (36)$$

$R^2 = 0.80$
$n = 28$

No observable trends were observed between $RGR_{S,leaf}$ and $w_{S,leaf}$. $RGR_{P,leaf}$ and $w_{P,leaf}$ were simulated using the mean mass of *S. megaphylla*, ($\overline{w}_{S,leaf}$), and Equations 35 and 36. The actual and simulated values of $RGR_{P,leaf}$ for treatments A, B, C, and D growing under different levels of *S. megaphylla* competition are illustrated in Figure 4.19.

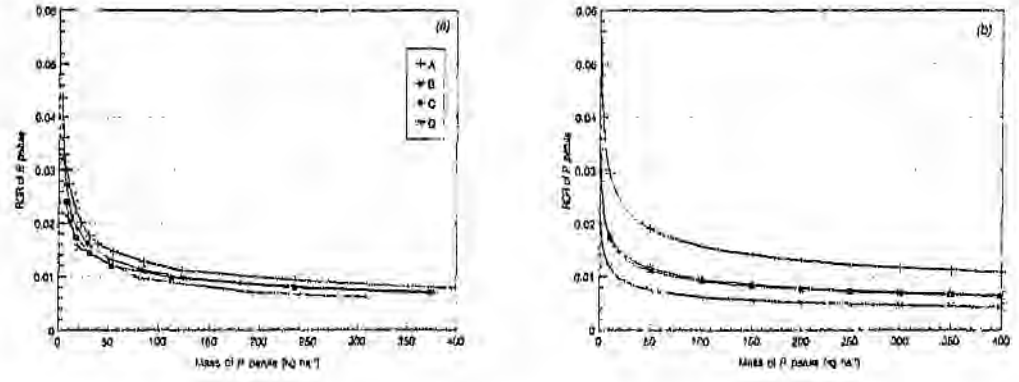


Figure 4.19. The actual (*a*) and simulated (*b*) values of $RGR_{P,leaf}$ for treatments A, B, C, and D growing under different levels of *S. megaphylla* competition as a function of the mass of *P. patula*.

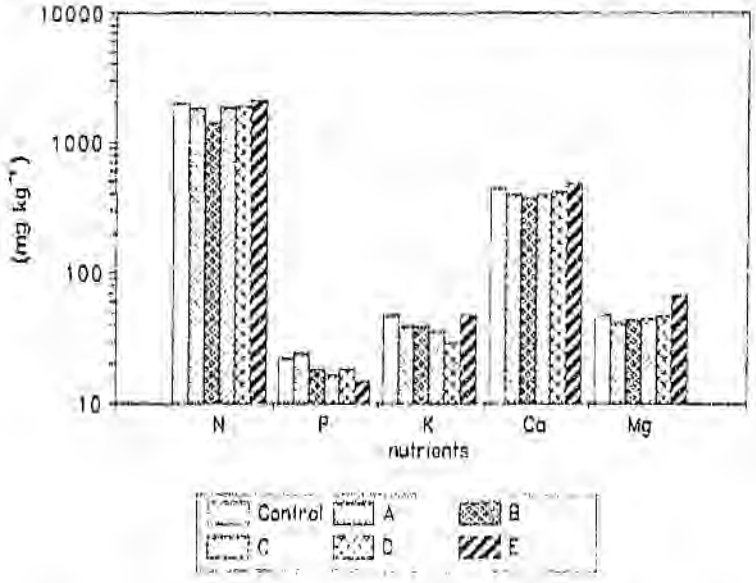


Figure 4.39. Differences in soil nutrient levels between the various treatments 21 months after establishment.

The treatment means (μg N g^{-1} day^{-1}) and standard deviations for nitrogen mineralization rates are given in Table 4.11. The rates of N mineralization were low and erratic, with the majority of samples showing no net mineralization at all. Treatment E, which underwent no clippings, had the highest mineralization rate of 0.13 μg N g^{-1} day^{-1}. This was significantly different to the remaining treatments.

Table 4.11. Means (μg N g^{-1} day^{-1}) and standard deviations for nitrogen mineralization rates for the six competition regimes.

Treatment	Mean	Std. Deviation
Control	0	-
A	0	-
B	0.04	0.05
C	0.03	0.03
D	0.07	0.08
E	0.13	0.02

Mineralization is generally high in substrates with high nitrogen contents and under environmental conditions favourable for microbial activity. Microbial immobilization tends to be high (lowering net mineralization) when nitrogen concentrations in organic matter are low. This is because a relative abundance of carbon compounds provides energy for using nitrogen to synthesize new microbial biomass (Brady 1974). The pooled organic carbon and nitrogen content of the A horizon (Table 3.2) is approximately 0.0118 g g^{-1} and 1290 mg kg^{-1} respectively. The C:N ratio is approximately 9:1, which

4.4 Competition for nutrients

4.4.1 Soil nutrients

The changes in soil nutrient status between September 1989 and July 1990 are illustrated in Table 4.10. Decreases in soil nitrogen were recorded in treatments A, B, C and E. This decrease was only significant for treatment B. There were increases in phosphorus in all treatments although this increase was not significant in treatment E. An increase in soil phosphorus might be due to the greater colonization of the soil profile by roots with a resultant increase in phosphorus- mineralization.

Potassium decreased in all treatments. Differences in potassium content were significant in treatments A, C, and D. Grey *et al.* (1979) and Payn (1985) identified potassium as one of the major elements influencing the growth of *P. patula*. Potassium is known to be important in osmotic adjustment and turgor maintenance (Sands and Mulligan 1990).

No significant changes occurred in soil calcium levels between the September 1989 and July 1990 enumerations. Magnesium concentrations decreased in all treatments although not significantly so in treatment D.

Table 4.10. Changes in soil nutrient status over time. Nutrient levels (mg kg^{-1}) are presented for September 1989 (d1) and July 1990 (d2). Double and single asterisk denote significance differences at the 5 and 10% level respectively. The sample sizes (N), means (mg kg^{-1}) and standard deviations are presented in Appendix 14.

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium	
Treatment	09/89	07/90	09/89	07/90	09/89	07/90	09/89	07/90	09/89	07/90
Control	1833.8	1979.5	8.2	22.0**	71.7	46.5	369.1	440.3	91.4	47.3**
A	2055.8	1816.3	8.8	23.8*	54.2	39.0**	380.8	394.5	107.9	41.0**
B	1843.3	1403.5*	7.6	18.0**	49.0	38.5	361.4	367.8	94.8	43.5**
C	1949.8	1844.8	7.4	16.3**	64.2	36.3**	359.9	388.5	96.8	44.8**
D	1843.3	1859.3	8.4	18.3**	60.4	28.8**	316.6	414.8	82.3	46.5
E	2095.3	2088.0	10.2	14.5	57.4	46.5	440.4	484.3	109.7	67.8**

In July 1990, 21 months after establishment, analysis of variance (ANOVA) between the different treatments showed that no significant differences in soil nutrient levels for nitrogen ($F_{5, 15} = 0.40$), phosphorus ($F_{5, 15} = 0.25$), potassium ($F_{5, 15} = 0.25$), calcium ($F_{5, 15} = 0.84$) and magnesium ($F_{5, 15} = 0.34$) occurred between the various treatments. Figure 4.39 illustrates the differences in soil nutrient levels between the various treatments 21 months after establishment.

S. megaphylla, at any particular time, the water-use efficiency would increase to approximately 1.97 g kg^{-1}. This derived value for water-use efficiency is lower than that of *P. patula*, indicating that *P. patula* is a more efficient user of water than *S. megaphylla*.

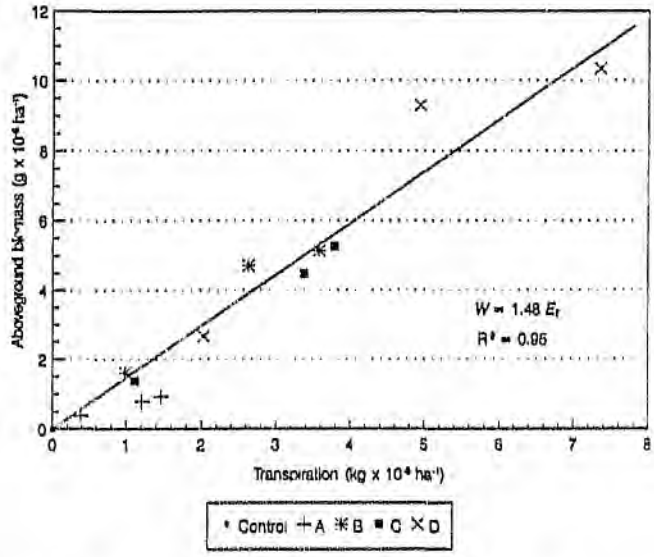


Figure 4.38. The water use efficiency for *S. megaphylla*. Treatment E is excluded as a result of insufficient samples.

Figure 4.37. Regardless of the level of competition, a distinct linear relationship exists. There is extensive evidence that for any one species, the seasonal water-use efficiency is constant over a wide range of treatments such as sowing date, planting density, and water and nutrient supply (Jones 1983). This linear relationship provides strong evidence that competition for water is the main causal factor limiting the productivity of *P. patula*. The water-use efficiency of *P. patula* is approximately 2.68 g kg^{-1} (g of biomass per kg of water used).

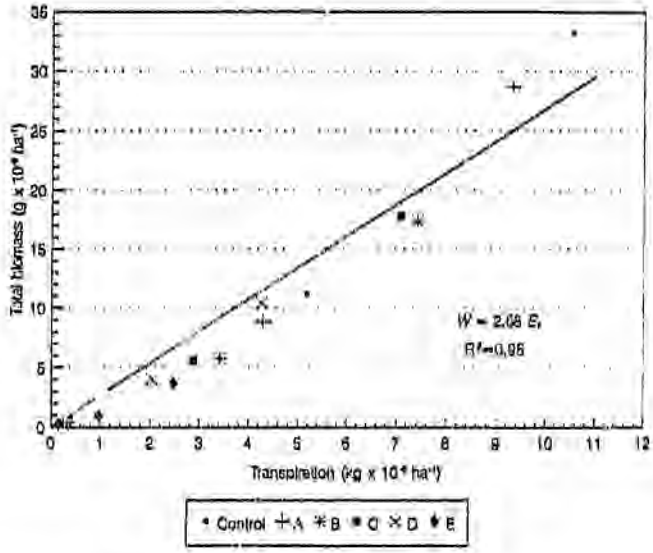


Figure 4.37. The water use efficiency for *P. patula*.

The cumulative aboveground biomass in relation to transpiration (E_T) of *S. megaphylla* is illustrated in Figure 4.38. As with *P. patula*, there is a strong linear relationship between the two variables. The highest E_T occurs in treatment D, which has the highest cumulative biomass. Treatment E was not included in this study as there were insufficient biomass samples. As with *P. patula*, the distinct linear relationship between the two variables provides strong evidence that competition for water plays an important role in reducing the productivity of *P. patula* .

The water-use efficiency of *S. megaphylla* was approximately 1.48 g kg^{-1} (g of aboveground biomass per kg of water). Root masses for the sampling periods were unavailable, and therefore no direct comparisons between the water use efficiencies of *P. patula* and *S. megaphylla* are possible. However, sampling of root mass was carried out at eight, 20 and 32 months of age (Figure 4.15). Although not the same dates, those root proportions can be used to estimate the total biomass of *S. megaphylla*. From the biomass samples, assuming that the η_{root} contributes 33% to the total biomass of

from the soil surface in treatment E contributed to 18% of the water balance. The low evaporation from treatment E is understandable as in this treatment *S. megaphylla* rapidly achieved canopy closure and was never clipped.

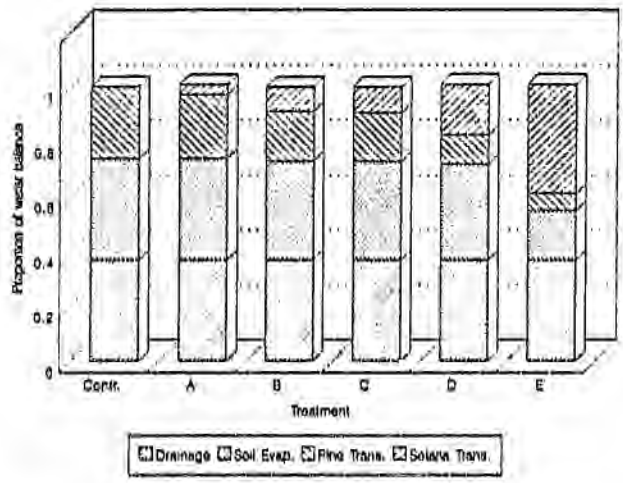


Figure 4.36. The proportions of water loss attributed to drainage, runoff, soil evaporation and transpiration from *P. patula* and *S. megaphylla*.

The peak rates of water use for *P. patula* occurred in the summer months of November to February and ranged from 6.2 mm day^{-1} (Control) to 1.7 mm day^{-1} (treatment E). Maximum transpiration rates for *P. patula* correspond closely with the 4-5 mm day^{-1} measured in five year old *P. patula* using the heat pulse velocity technique (Dye[5] *pers comm* 1995). The peak rates of water use for *S. megaphylla* occurred in the same months. Daily transpiration rates ranged from 2.7 mm day^{-1} (treatment A) to 5.7 mm day^{-1} (treatment E). The transpiration of *P. patula* as a proportion of the water balance clearly reflected the competition regimes. Proportionally, transpiration was highest for *P. patula* in the Control (26% of the total water balance), and lowest in treatment E (6%). Expectedly, the transpiration as a proportion of the water balance demonstrated the reverse trend, namely lowest in treatment A (4%) and highest in treatment E (40%). Over the study period the soil water declined by approximately 1%.

4.3.7 Water-use efficiency

The relationship between the total biomass (W) and the transpiration (E_T) for *P. patula* is illustrated in

[5]P.J. Dye, FORESTEK, Private Bag X11227, Nelspruit, South Africa.

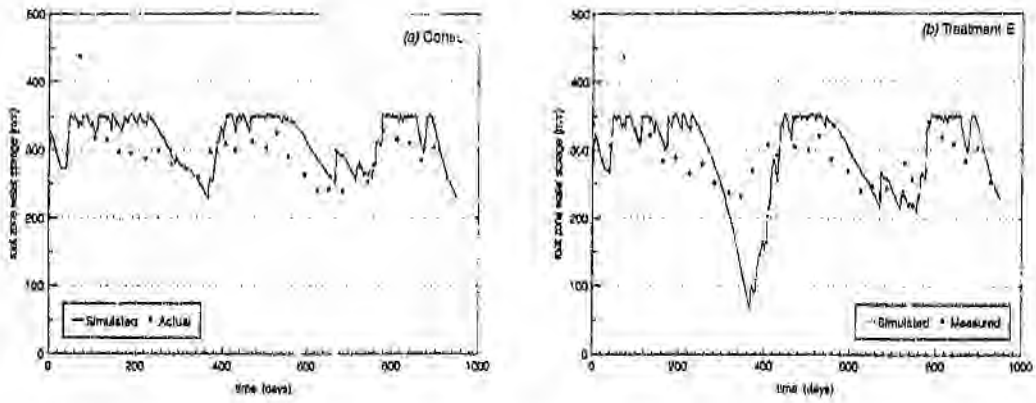


Figure 4.35. Simulated and measured soil water contents in the upper 1.5 m of the soil profile, expressed as depth equivalents over 947 days for *(a)* Control and *(b)* Treatment E.

The water balance for the treatments over a period of 947 days is presented in Table 4.9. The proportional contribution of runoff, drainage, and transpiration by *P. patula* and *S. megaphylla* are presented in Figure 4.36. Rainfall for the period was 4043 mm. This equates to 1122 mm for first year, 1548 mm for the second year and 1374 mm for the latter 7 months. The simulations indicated that no runoff occurred. Drainage until May 1991 was approximately 1500 mm for all treatments.

Table 4.9. The water balance (mm) from 18 October 1988 until 24 May 1991.

Trt	Rain	Runoff	Drainage	Evap. (soil)	Transp. (*P. patula*)	Transp. (*S. megaphylla*)	Soil store
Control	4043	0	1500	1507	1054	0	-16.8
A	4043	0	1499	1484	931	146	-16.7
B	4043	0	1500	1461	741	358	-16.8
C	4043	0	1498	1475	708	379	-16.7
D	4043	0	1499	1401	426	734	-16.8
E	4043	0	1497	714	247	1603	-17.0

Drainage accounted for approximately 37% of the water balance. The granite derived soils on which this trial is laid out are very well drained. The surface horizons tend to have a low water holding capacity. This is mainly due to a high content of medium to coarse sand and a strong aggregation of clay particles into water stable micro-aggregates. This results in a high frequency of macro-pores. In combination with the non-expanding properties of the kaolinite clays, this causes rapid drainage (Schutz 1990).

Evaporation from the soil surface is influenced by the combined leaf area of *P. patula* and *S. megaphylla*. Simulated evaporation ranged from 1507 mm in the Control, to 714 mm in treatment E. Evaporation from the soil surface was approximately 37% for all treatments except for treatment E. The evaporation

4.3.6 Water Balance

The daily net radiation over the study period is shown in Figure 4.34. Where there are missing values, the 10 day average prior to the missing values was calculated and substituted. A definite cyclic trend is apparent, with the greatest amount of net radiation occurring during the summer.

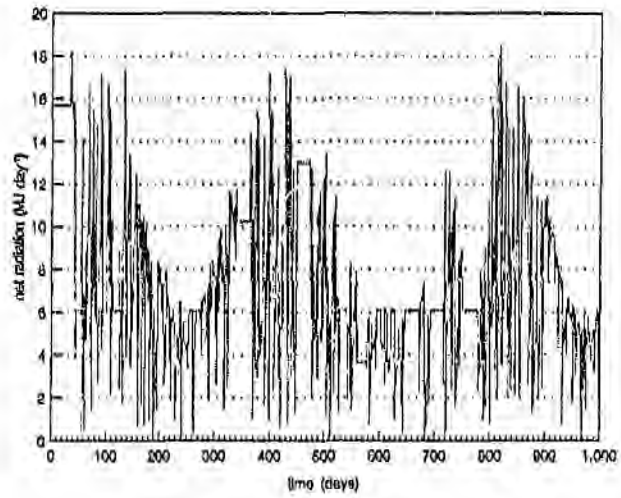


Figure 4.34. The daily net radiation for the study period.

The simulated and measured soil water contents in the top 1.5 m of the soil profile for the Control and treatment E, with their respective L and η_{root} are shown in Figure 4.35. Generally, although not a good fit, the simulated root zone water storage follows the same trends as the measured values. The seasonal decreases in root zone water storage are clearly apparent for both treatments. These decreases correspond to decreases in the annual rainfall (Figure 4.23). The simulated winter decreases are more pronounced than the actual values. The decreases are greater and for a longer duration in treatment E compared to the Control. This implies that not only is the available water less under the highest competition regime, but the soil profile of the root zone takes longer to "recharge". Treatments A, B, C and D follow the same trends, also having decreasing amounts of water in the root zone during the winter months.

variable than *P. patula*. This is most probably due to the different clipping schedules and the resultant variability in leaf ontogeny. As with *P. patula*, stomatal conductances for *S. megaphylla* in March were higher than those recorded for July. Although difficult to ascertain due to the variability, maximum stomatal conductance appeared to occur over a longer period of the year. Stomatal conductances for *P. patula* were much lower than *S. megaphylla*. If it is assumed that stomatal behaviour reflects the rate of supply of water to the leaves and subsequent biomass production, then *S. megaphylla* is more efficient in this respect than *P. patula*.

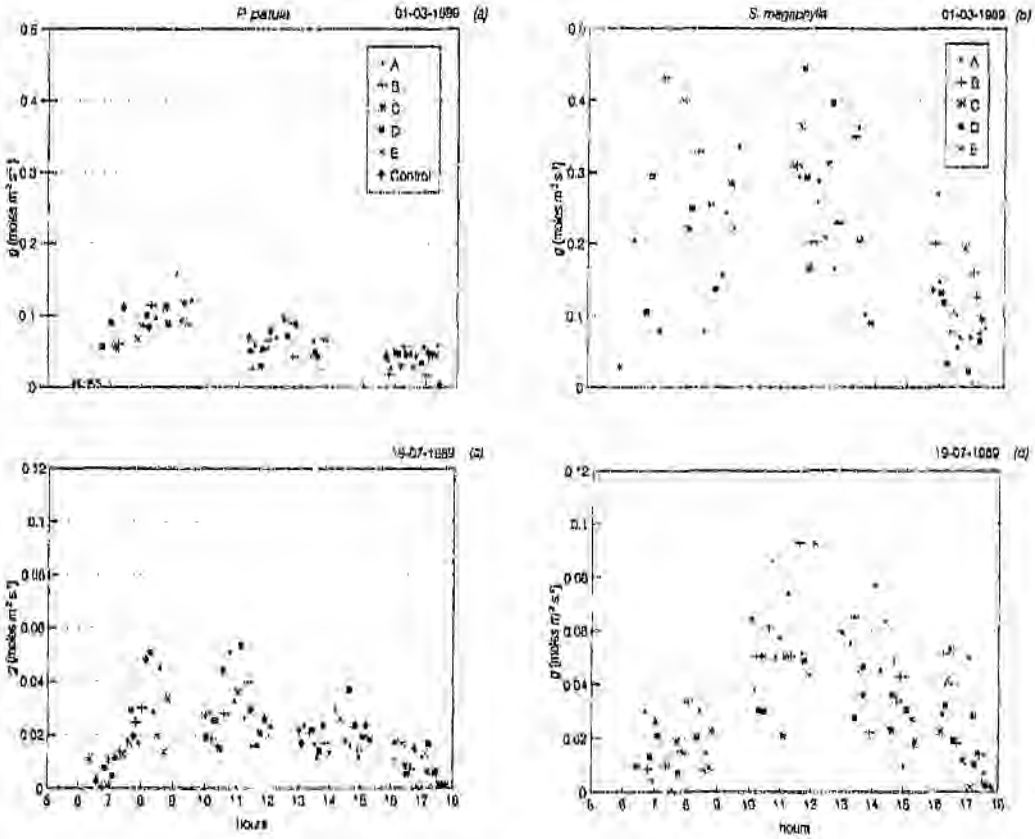


Figure 4.33. Stomatal conductances measured over the course of a day for (*a*) *P. patula* in March, 1989, (*b*) *S. megaphylla* in March 1989, (*c*) *P. patula* in July 1989 and (*d*) *S. megaphylla* in July 1989.

An attempt was made to examine the relationship between diurnal plant water potential and stomatal conductance. This relationship was poorly defined and is therefore not illustrated. The variability in the data probably relates to the effects of variations in vapour saturation deficit and mean air temperature (Boadle *et al.* 1986).

The relationship of d_c and aboveground biomass to $S\psi$ provides strong evidence that competition for water is occurring. The correspondingly greater accumulated water stress in *P. patula* growing under high competition regimes therefore results in lower productivity.

As a comparison, the cumulative aboveground biomass of *S. megaphylla* biomass is shown in Figure 4.32. There is a very poor relationship between the aboveground biomass of *S. megaphylla* and the cumulative $S\psi$, and it appears as if water is not affecting the growth of *S. megaphylla*. Root studies (Section 4.1) indicate that *S. megaphylla* is able to access water from far greater depths in the soil profile.

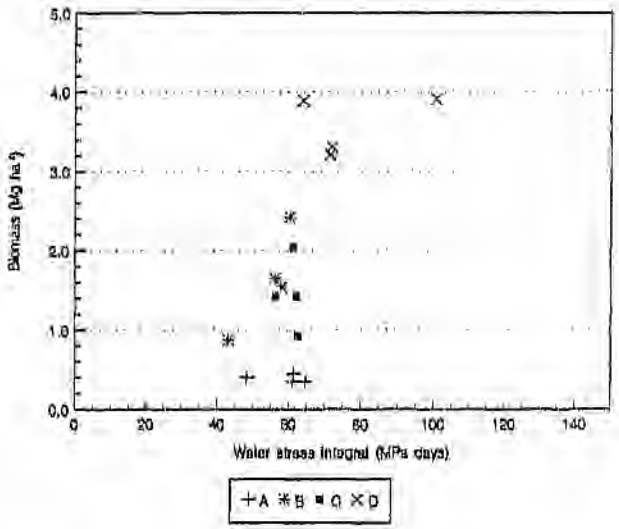


Figure 4.32. The cumulative biomass of *S. megaphylla* in each treatment as a function of the cumulative $S\psi$, for the first year of the study.

4.3.5 Stomatal conductances

Figures 4.33a and c show the diurnal stomatal conductances for *P. patula* in March and July respectively. No distinct trends between the various competition regimes for *P. patula* are observable. Stomatal conductances for *P. patula* were highest in March, and reached their maximum levels of 0.09 to 0.16 moles m^{-2} s^{-1} between 08h00 and 10h00. The highest stomatal conductances for *P. patula* in July were between 0.03 and 0.05 moles m^{-2} s^{-1}, and occurred between 08h00 and 11h30.

The diurnal stomatal conductances for *S. megaphylla* for the same months are illustrated in Figures 4.33b and d. The stomatal conductances of *S. megaphylla* for the different treatments were more

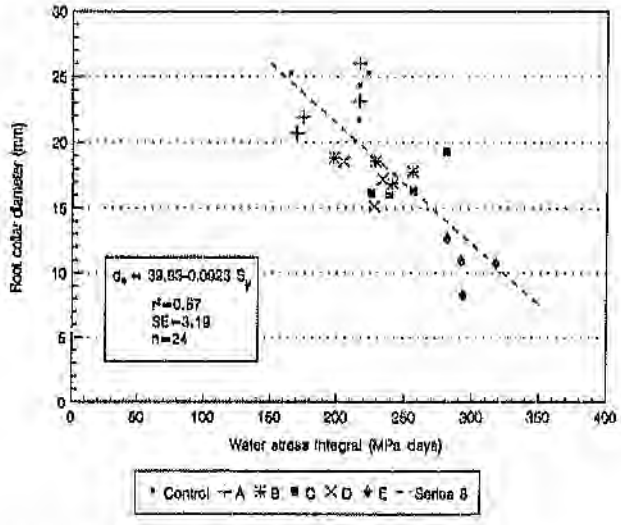


Figure 4.30. The root collar diameter (d_c) of *P. patula* in each treatment as a function of the cumulative $S\psi$, for the first year of the study.

Figure 4.31 shows the aboveground biomass of *P. patula* for each treatment and replication 336 days after establishment as a function of the cumulative $S\psi$. Although the coefficient of determination is low (0.39), a linear trend is also apparent. The larger the cumulative $S\psi$, the smaller the biomass becomes. Highest biomasses and lowest $S\psi$ occur in the Control, followed by treatment A. Lowest biomasses and $S\psi$ occur in treatment D followed by treatment E.

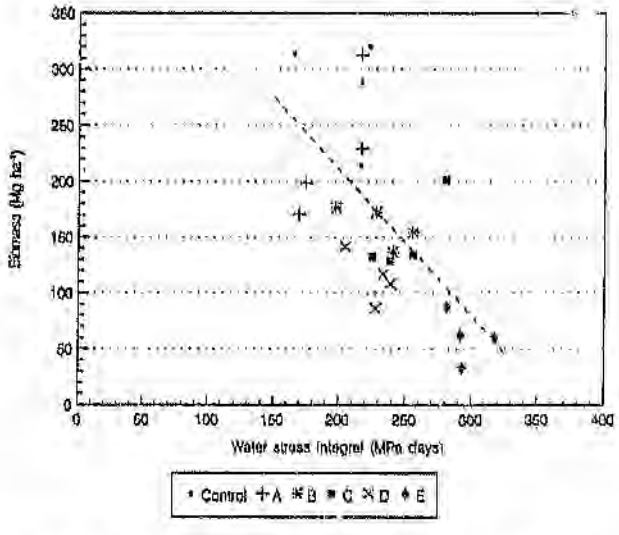


Figure 4.31. The biomass of *P. patula* in each treatment as a function of the cumulative $S\psi$, for the first year of the study.

highest. Generally, for the same sampling date, the $S\psi$ for *S. megaphylla* was much lower than the $S\psi_s$ indicating far less cumulative water stress.

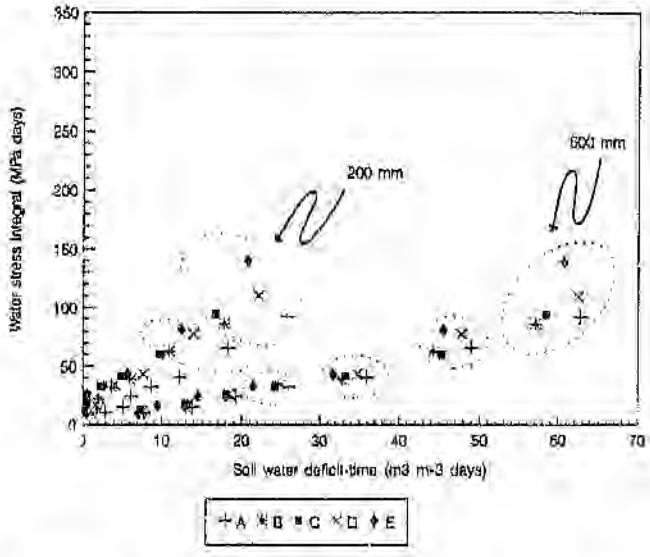


Figure 4.29. The cumulative $S\psi$ of *S. megaphylla* in each treatment as a function of the cumulative soil water-deficit-time for the first year of the study. The different treatments for a particular sampling date are encircled.

As θ_s and consequently $\theta_{def\text{-}time}$ fluctuates within the soil profile, the use of $\theta_{def\text{-}time}$ in conjunction with $S\psi$ as an indicator of the response of trees to changes in θ_s is not always reliable. A more reliable indicator appears to be between $S\psi$ and some measure of plant productivity.

Figure 4.30 shows mean d_c as a function of cumulative $S\psi$ after 336 days, for all replications and treatments. Although the coefficient of determination is only 0.67, there is a linear relationship between d_c and $S\psi$. Trees with the highest d_c have the lowest $S\psi$ values, and occur either in the Control or treatment A. Treatment E has the lowest d_c and the highest $S\psi$ values.

The value of the linear relationship between $S\psi$ and $\theta_{def\text{-}time}$ is in the fact that the soil water deficits can be calculated from atmospheric conditions, rainfall and an understanding of soil water retention characteristics. They can therefore be used in a predictive sense, i.e.

$$S\psi = f(\theta_{def\text{-}time}) = a + b(\theta_{def\text{-}time}) \qquad (37)$$

potential values close to those at pre-dawn were much faster for *S. megaphylla* (Figure 4.27.d) than for *P. patula*, (Figure 4.27c).

4.3.4 Water stress integrals

Figure 4.28 shows the relationship between the cumulative water stress integral ($S\psi$) and the cumulative soil water deficit ($\theta_{def\text{-}time}$) for *P. patula* at depths of 200 and 600 mm for the sampling intervals shown in Table 3.6. For a particular treatment and position in the soil profile, the $S\psi$ increases with time and with increasing $\theta_{def\text{-}time}$. These differences become more apparent with time. For the last two sampling dates, the $S\psi$ for the Control and treatment A are much lower than the remaining treatments, with the $S\psi$ in treatment E being the highest. The differences between the highest and lowest $\theta_{def\text{-}time}$ for the 200 and 600 mm intervals is approximately 6 and 7 $m^3\ m^{-3}$ days respectively, and no clear trends are apparent. The higher $\theta_{def\text{-}time}$ values in the treatments growing under the lowest competition are a result of earlier, lower θ_s values. For the same $S\psi$ values, differences in $\theta_{def\text{-}time}$ occur at the two depth classes. The $\theta_{def\text{-}time}$ for any particular sampling date is higher at the 600 mm than at the 200 mm depth. This is obvious as the θ_s at the 600 mm level is always lower than at the 200 mm level.

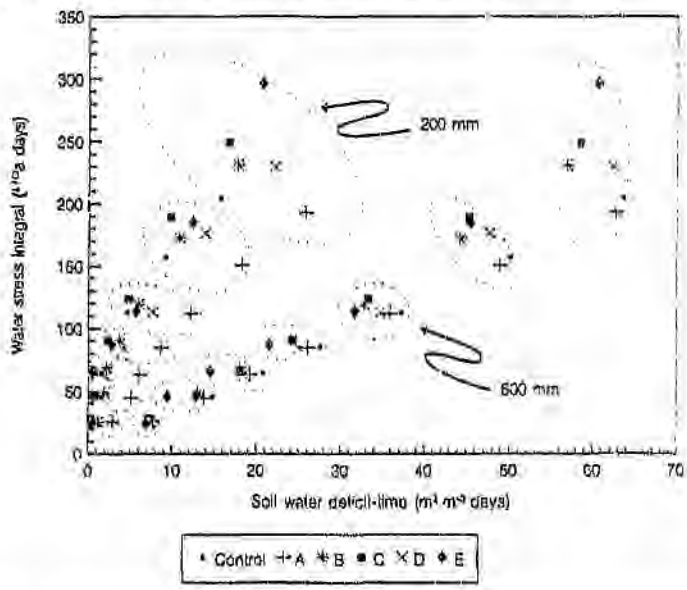


Figure 4.28. The cumulative $S\psi$ of *P. patula* in each treatment as a function of the cumulative soil water-deficit-time for the first year of the study. The different treatments for a particular sampling date are encircled, with the earliest sample dates closest to the origin.

Similar relationships occur for *S. megaphylla* (Figure 4.29). For the last two sampling dates at both the 200 and 600 mm depth, treatments A, B and C had the lowest $S\psi$ and the treatments D and E the

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sampling are notoriously difficult. Methods for determining configuration such as the use of rubidium should be appraised. Root periscopes in conjunction with videogrammetry should be considered for determining root densities.

Plant water potential measurements do provide some measure of the plant water status and the degree of stress that a plant experiences. The use of plant water potential is not always satisfactory, both from a logistics point of view (frequency and intensity of sampling) and because measurements fail to integrate easily between water stress and growth over time. Water studies should focus on more effective ways of determining transpiration rates of young trees. Heat pulse velocity techniques should be evaluated.

The conventional approach to nutrient analyses in this trial yields baseline information and bears little relation to the capacity of the soil to provide nutrients or indications of the biogeochemical cycles of each element. Future research should focus on rates of mineralization, the dynamics of translocation and retranslocation in needles and shoots and the complex interactions between nutrient uptake and soil moisture content.

In conclusion, the approach followed in this study has led to a far more detailed understanding of the effects and underlying processes between *P. patula* and *S. megaphylla*. It is hoped that this study will contribute to a sound, site specific weed management strategy for plantation forestry in South Africa.

The studies of soil water content, pre-dawn plant water potential, water stress integral and water-use efficiency provide strong evidence that competition for water is the most limiting factor in the growth of *P. patula* and that even small differences in water stress can affect the early growth of *P. patula*. As competition for water occurs at specific times, the timing of weed control could be an important component of a weed management strategy.

No significant difference in the soil macronutrients, nitrogen, phosphorus, potassium, calcium and magnesium occurred between treatments 21 months after establishment. In all treatments, soil potassium and magnesium decreased by as much as 60% over time. Soil calcium increased slightly and phosphorus status more than doubled. Significant differences between the treatments with respect to foliar concentrations of phosphorus, potassium and magnesium for *P. patula* occurred 21 months after establishment. Lowest potassium levels occurred in the treatments subjected to highest competition regimes (treatments C, D and E). Foliar magnesium levels increased with increasing competition.

Vector analyses supports the hypotheses that competition for water is the most important factor with respect to reducing the growth of *P. patula* and that secondary to competition for water is competition for nutrients and for light.

The approach followed in this study has led to a greater understanding of the competitive effects of *S. megaphylla* on the growth of *P. patula*. In addition it has provided invaluable guidance as to the design and methodology of future competition trials. Trial design should always focus on the creation of a range of competition regimes in order to elicit responses and develop an understanding of the reasons for the responses. In addition to a Control where *P. patula* were kept free of any weed competition, a treatment with only *S. megaphylla* should be considered. This would then provide a complete range of competition regimes. Better techniques should be adopted for assessing the leaf area of *S. megaphylla* and *P. patula*. More frequent biomass sampling of treatment E in the destructive sampling zone is also recommended.

The frequency of measurements is most important. In many competition trials, the effect of weed competition is most commonly measured on a quarterly, six monthly or annual basis. A higher frequency of measurements, especially during the first year after establishment is recommended as infrequent measurements could conceal the dynamics of competition.

Priority for future research on growth should focus on issues pertaining to carbon allocation, belowground dynamics (root studies), and foliage dynamics. By far the biggest challenges lie in root studies. Without a better understanding of the contribution roots make to the total biomass of a tree little progress can be made in developing models of carbon allocation. The practicalities in root

reduced by either competition for water or for nutrients.

Values for light-use efficiency for *S. megaphylla* are greater than for *P. patula*. In addition, there is less differentiation in light-use efficiency between treatments indicating that competition for light is an important factor in determining the growth of *S. megaphylla*.

Soil moisture trends closely follow rainfall events. Approximately one year after establishment, clear differences in soil water content in the lower levels of the soil profile were recorded for the different treatments. Trees growing under the highest competition regimes (treatments D and E) had the lowest soil water contents. As the trees grew older, the differences in the soil water content between the various treatments decreased. It is suggested that at this stage, intraspecific competition for water in the low competition regimes is having a similar effect when compared to interspecific competition at the high competition regimes.

Patterns in soil water content at different depths were remarkably consistent. In all treatments, and at all depths, as the dry season progressed decreases in soil moisture occurred. The decreases in soil moisture were greatest under the highest competition regimes.

These differences in soil moisture were manifested in pre-dawn plant water potential readings. Decreases in the pre-dawn plant water potential coincided with decreases in soil water content. The greatest decrease in pre-dawn plant water potential for *P. patula* occurred under the highest competition regimes. The pre-dawn plant water potentials for *P. patula* were more negative than for *S. megaphylla*.

In order to assess the cumulative effect of water stress on the growth of *P. patula*, the water stress integral as a function of soil water content, root collar diameter and biomass was examined. For a particular treatment and depth in the soil profile, the water stress integral increased with time and with the cumulative soil water deficit. The differences became more apparent with time. A linear relationship exists between root collar diameter and the water stress integral. Trees with the greatest root collar diameters have the lowest water stress integral. The same trends are apparent for biomass. This implies that trees growing under lower water stress have greater rates of growth.

Water-use efficiencies for *P. patula* growing under the different competition regimes was determined by examining the relationship between cumulative transpiration and biomass production. The water-use efficiency was constant over the range of treatments. For example, the higher the transpiration, the greater the biomass production and *visa versa*. The water-use efficiency for *P. patula* was approximately 20% greater than that of *S. megaphylla*.

more site specific approach to weed management and thinnings should be considered.

With respect to belowground parameters, the different competition regimes are clearly expressed by the differences in the root mass, length and configurations of *P. patula* and *S. megaphylla*. As an example, root densities of *P. patula* 32 months after establishment, growing under low competition regimes were between three and four times greater than under the highest competition regime. The density of *S. megaphylla* growing in the highest competition regime (treatment E) was more than eight times that of *P. patula* growing in the Control. In absolute terms, after 32 months, *S. megaphylla* was able to 'colonize' a far greater proportion of the soil profile compared to *P. patula*. Whereas after 32 months following establishment between 38 and 78% of *P. patula* roots occurred in the top 300 mm of the soil profile, the percentage of *S. megaphylla* roots in the top 100 mm ranged from 66 to 88%.

The biomass studies and more specifically the proportion of carbon allocated to each of the biomass components of *P. patula* demonstrates the dynamics of the carbon allocation strategy. Carbon allocation depends on the levels of competition at any particular time. This dynamic situation is reflected in the change in coefficient values in the allometric equations with different levels of competition, the difference in root configurations and the changes in the proportions of root , stem, branch and needle biomass in relation to the total biomass of *P. patula* . The biomass studies also demonstrate the importance of including the belowground component. Excluding the roots from biomass allocation studies can lead to the misinterpretation of results.

There is a linear relationship between $RGR_{P,leaf}$ and $RGR_{S,leaf}$ which provides for interpretive problems. For a given $RGR_{S,leaf}$, the $RGR_{P,leaf}$ increases with decreasing levels of competition. No relationships were found between the $RGR_{P,leaf}$ and $w_{S,leaf}$ at any particular time. It was hypothesized that the differences are a result of either the frequency of clipping carried out for each treatment, or the mean mass of *S. megaphylla* that occurs for a particular treatment over the duration of the study period.

A function describing the interaction between *P. patula* and *S. megaphylla* was developed. The mean mass and relative growth rate of *S. megaphylla* foliage were the most important variables in describing the relative growth rate of *P. patula* leaves. With the knowledge of the foliar mass of *P. patula* and the proportions of each biomass component at a specific time, it is possible to determine the mass of each of the component.

The possible causal effects of competition were also investigated. For *P. patula* there is an inverse relationship between the level of competition and light use efficiency. Treatments with little or no competition from *S. megaphylla* had the highest growth efficiencies. Results indicate that for *P. patula*, competition for light is not limiting the growth of trees and that the efficiency of light use is

5. CONCLUSION

Most research in plantation weed management in South Africa has focused either on the autecology of the weed species or the empirical comparison of different control methods. Although such studies can help researchers develop new technologies and demonstrate the impact of weed control on survival and growth, the studies have not provided a quantitative basis by which plantation managers can make effective weed management decisions. Neither has the research provided much insight into the mechanisms of competition.

Four main objectives were set in the three year study of the competitive effects of *S. megaphylla* on the growth of *P. patula*, namely:

- the degree to which *S. megaphylla* suppresses the growth of *P. patula*;
- the level of *S. megaphylla* infestation necessary for the suppressive effect to occur;
- the duration of the suppressive effect by *S. megaphylla* on *P. patula*; and
- the possible reasons why *S. megaphylla* inhibits the growth of *P. patula*.

The field trial showed that *S. megaphylla* does suppress the growth of *P. patula* and that suppression was strongly correlated with the biomass of *S. megaphylla*. The impact was most clearly reflected in the aboveground growth parameters of *P. patula*, namely height, root collar diameter, volume index, needle length and biomass.

As examples, after three years, the height of *P. patula* growing under the lowest competition regimes was approximately 35% greater than for trees growing under the lowest competition regimes. This is a difference of more than 2 m in height. Root collar diameter was approximately 40% greater in *P. patula* growing under low competition regimes, a difference of almost 60 mm.

The relative growth rates of *P. patula* provided interesting insights into the responses of *P. patula* to different levels of competition. Relatively small differences in relative growth rate can lead to much larger, absolute exponential differences in early growth. Perhaps of more relevance is how relative growth rates calculated at frequent intervals can provide indications of the transition from interspecific to intraspecific competition. Indications are that depending on the level of weed competition, intraspecific competition can occur as early as two years after establishment on this particular site. This suggests that the effect of early weed control might be negated by the onset of intraspecific competition. Current thinning regimes in South Africa tend to be prescriptive. Normally first thinnings take place between seven and eight years of age, irrespective of the site index or level of weed competition. The early responses achieved from weed control would therefore be nullified. The study suggests a much

The vector analyses support the hypothesis that competition for water is the most important factor reducing the growth of *P. patula*. Secondary to competition for water is competition for nutrients and light.

The contents of magnesium in all treatments relative to the Control are less and clearly reflect the competition regime. The relative content is greatest in treatment A and lowest in treatment E. This implies that growth reductions are a result of reduced nutrient uptake. This reduced uptake is most likely due to increased competition for water.

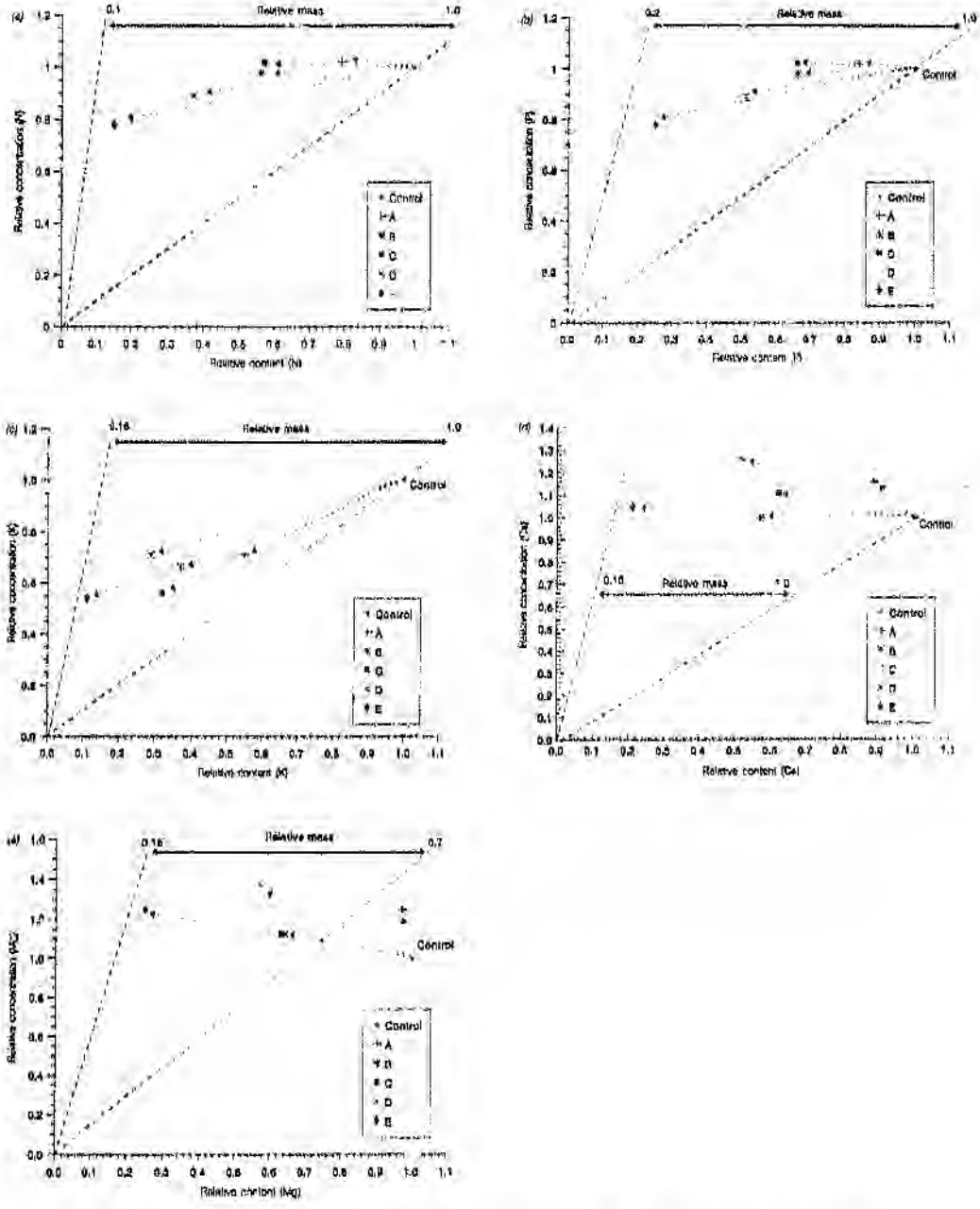

Figure 4.42. Vector analysis diagrams for *(a)* nitrogen, *(b)* phosphorus, *(c)* potassium, *(d)* calcium and *(e)* magnesium.

4.4.3 Vector analyses

Figure 4.42 shows the vector analyses for nitrogen, phosphorus, potassium, calcium and magnesium for September 1989. The relative masses reflect the different competition regimes. The mass of foliage in treatment A relative to the Control is the highest. Treatment E has the lowest mass relative to the Control.

There is little difference in the concentration of nitrogen for treatments A, B and C relative to the Control (Figure 4.42a). The relative nitrogen content of these treatments is lower due to the decrease in foliage mass. This implies that nutrient uptake, but not concentration, is reduced by moisture stress, and that growth is more likely to be limited by competition for water rather than nutrients. Treatments D and E, subject to the highest competition regimes, show a decrease in the concentration and content of nitrogen relative to the Control. Growth reduction is caused by both competition for water and secondarily by competition for nitrogen.

The relative concentrations and relative contents for phosphorus (Figure 4.42b), display similar trends as shown for nitrogen. Relative to the Control, the growth of trees in treatments A, B and C are reduced as a result of decreases in the uptake of phosphorus. These reductions in the uptake of phosphorus can be ascribed to increased water stress. Treatments D and E have lower concentrations and contents of phosphorus relative to the Control. In these treatments, competition for both water and phosphorus is limiting growth.

For all treatments, the concentration and content of potassium shows decreases relative to the Control (Figure 4.42 c). The greatest decreases in relative content occur in treatments C, D and E. No trends between treatments in the relative concentrations of potassium are apparent. As discussed earlier, the availability of potassium depends on the θ_s (Grey *et al.* 1979, Payn 1985 and Sands and Mulligan 1990). Reductions in growth in the treatments are likely to be a result of competition for both water and potassium.

The relative concentrations of calcium (Figure 4.42 d), are greater than or equal to the Control. No trends in relative concentration with respect to competition regimes are apparent. The relative contents of calcium in all treatments are lower than the Control. A trend which conforms with the competition regimes is apparent, namely the highest relative content occurs in treatment A and the lowest in treatment E. In all treatments, growth is reduced as a result of decreased nutrient uptake caused by increased competition for water.

The vector analyses for magnesium (Figure 4.42 e) show greater concentrations relative to the Control.

The differences in *S. megaphylla* foliar nutrient levels between the various treatments 21 months after establishment are illustrated in Figure 4.41. For comparative purposes the respective nutrient analyses are grouped together.

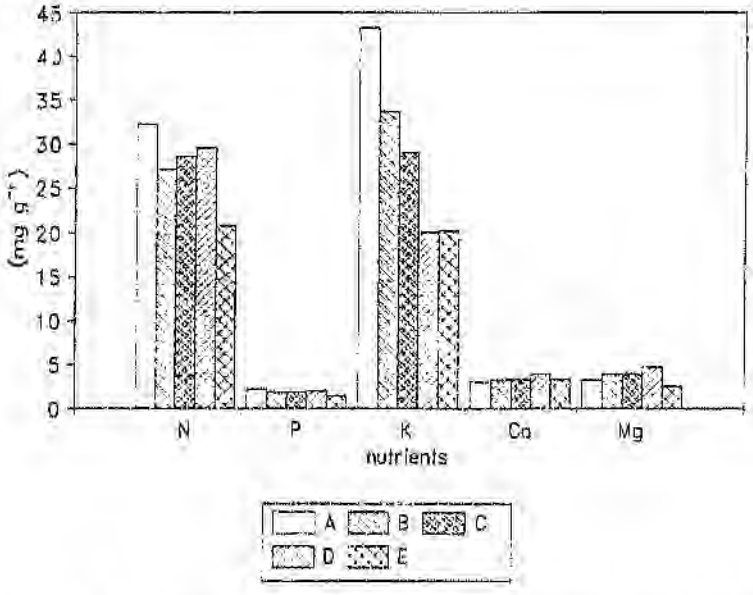

Figure 4.41. The differences in *S. megaphylla* foliar N, P, K, Ca and Mg levels for the various treatments 21 months after planting.

Significant differences occurred in foliar nitrogen for *S. megaphylla* ($F_{4,11}$ = 7.45**). Foliar nitrogen in treatment E was significantly lower than all the other treatments. This same trend was observed 11 months after planting (Table 4.12b). The highest potassium concentrations occurred in treatment A (43.0 mg g^{-1}) and the lowest in treatment D (20.1 mg g^{-1}). These potassium concentrations were not significantly different due to the high degree of variation within samples. No significant differences in foliar phosphorus ($F_{4,11}$ = 2.34), potassium ($F_{4,11}$ = 1.70), calcium ($F_{4,11}$ = 0.56) or magnesium ($F_{4,11}$ = 1.38) occurred.

There is a strong suggestion that potassium is a limiting nutrient to the growth of *P. patula*. The levels of foliar potassium in *P. patula* are below known critical levels reported in the literature (Schutz 1989). Except for treatment E, there is a distinct relationship between the degree of competition and levels of potassium.

Table 4.12. Foliar nutrient levels (mg g^{-1}) for September 1989 (d1) and July 1990 (d2) for (a) *P. patula* and (b) *S. megaphylla*. Double and single asterisks denote significance differences at the 5 and 10% level respectively. The sample sizes (N), means (mg g^{-1}) and standard deviations are presented in Appendix 15 and 16.

Table 4.12a. *Pinus patula*

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium	
Treatment	09/89	07/90	09/89	07/90	09/89	07/90	09/89	07/90	09/89	07/90
Control	17.5	13.7**	1.2	1.0**	4.1	4.6	1.9	2.4	0.8	0.8**
A	17.8	13.6**	1.3	1.1**	2.9	3.8**	2.2	2.6	1.0	0.8
B	17.2	14.0**	1.4	1.3	2.7	3.4**	1.9	2.4	0.9	0.8**
C	17.8	13.2**	1.4	1.2*	2.3	2.5	2.1	2.3*	0.9	0.8*
D	15.6	13.7	1.5	1.2	2.9	1.8	2.4	2.7	1.1	1.0
E	13.7	13.5	1.5	1.2	2.2	3.2*	2.0	2.6	1.0	1.0

Table 4.12b. *Setaria megaphylla*

	Nitrogen		Phosphorus		Potassium		Calcium		Magnesium	
Treatment	09/89	07/90	09/89	07/90	09/89	07/90	09/89	07/90	09/89	07/90
A	31.3	32.2	2.0	2.1	33.5	43.2	2.2	3.0	2.6	3.2
B	31.8	27.3*	2.3	1.8**	51.7	33.7**	1.5	3.3**	2.1	3.9**
C	26.4	28.6	2.0	1.9	47.4	29.0	2.2	3.3*	2.9	3.9
D	23.4	29.5	1.5	2.0*	20.0	20.1	2.9	3.8	3.0	4.7
E	19.5	20.7	1.0	1.4	19.5	20.3	2.2	3.3**	1.8	2.5*

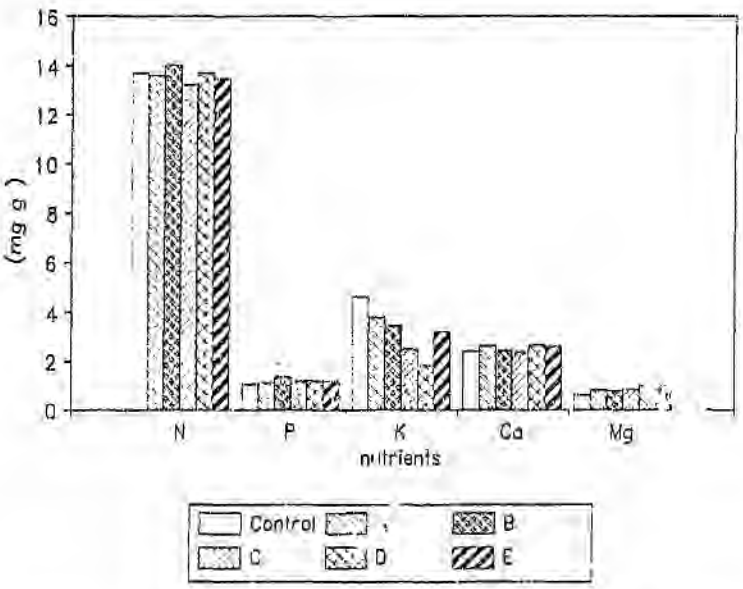

Figure 4.40. The differences in *P. patula* foliar N, P, K, Ca and Mg levels for the various treatments 21 months after planting.

suggests immobilization of nitrogen. The nitrogen immobilisation was most probably due to the large amount of freshly dead organic material, such as severed roots, in the incubation tubes.

4.4.2 Foliar nutrients

Tables 4.12a and b illustrate the changes in foliar nutrient levels of *P. patula* and *S. megaphylla* between September 1989 and July 1990. In all treatments, decreases in foliar nitrogen, phosphorus and magnesium and increases in foliar potassium and calcium for *P. patula* occur. Significant decreases in foliar nitrogen are apparent for *P. patula* growing under the lower competition regimes (Control and treatments A, B and C). Similar trends were observed for foliar phosphorus and magnesium. Significant decreases in phosphorus levels occurred for the Control and treatments A and C. Magnesium concentration decreased significantly for treatments B, C and Control. Increases in foliar potassium for *P. patula* were significant for treatments A, B and E. These increases are in direct contrast to soil potassium content. The increases in foliar calcium for *P. patula* was only significant for treatment C a the 10% level.

No definite conclusions can be drawn from the foliar nutrient analysis of *S. megaphylla*. Significant decreases in foliar nitrogen, phosphorus and potassium concentration occurred in treatment B. Significant increases in calcium occurred in treatments B, C, and E.

The differences in *P. patula* foliar nutrient levels between the various treatments 21 months after establishment are illustrated in Figure 4.40. No significant differences occurred in foliar nitrogen ($F_{5, 15}$ = 0.27) and calcium ($F_{5, 15}$ = 0.48) between the various treatments. The level of foliar phosphorus in treatment B was significantly higher than in treatment A and the Control ($F_{5, 15}$ = 2.71*), which in turn were lower than treatments C, D and E. Levels of foliar potassium in the Control were significantly greater than treatments B, C, D and E ($F_{5, 15}$ = 11,96***). Potassium levels in treatment A were significantly less than in treatments C and D. Lowest foliar potassium levels in *P. patula* appear to occur in treatments under the highest competition regimes namely treatments C, D and E. Levels of foliar magnesium for *P. patula* were significantly different ($F_{5, 15}$ = 4.90***). In contrast to potassium, levels of magnesium increased with increasing competition. Levels of magnesium in treatments D and E were significantly greater than in treatments B and K. Differences in magnesium levels between treatments A, B and Control; were not significant.

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Appendix 6. Sample size (N), means, standard deviations and minimum and maximum values for w_{stem}, w_{branch}, and w_{needle} and η_{stem}, η_{branch}, and η_{needle}.

AGE=0.67 TMT=A

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	5	85.9200000	34.1822973	35.1800000	117.4000000
STEMM	5	15.1160000	5.7128246	8.0800000	21.1100000
BRANCHM	5	15.5840000	9.5060418	4.6800000	25.5400000
NEEDLM	5	55.2180000	20.3727685	22.4100000	74.6800000
STEMPRO1	5	0.1846971	0.0444453	0.1191209	0.2296760
BRCHPRO1	5	0.1686182	0.0477630	0.1163427	0.2245275
NEEDPRO1	5	0.6466834	0.0402499	0.6081772	0.7110151

AGE=0.67 TMT=B

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	5	97.1980000	23.5892734	70.9600000	134.2700000
STEMM	5	19.1360000	5.4920879	13.8400000	25.6700000
BRANCHM	5	14.1660000	4.4614437	9.0000000	21.2400000
NEEDLM	5	63.8960000	16.3859804	42.4700000	88.5700000
STEMPRO1	5	0.1980331	0.0398542	0.1619092	0.2536561
BRCHPRO1	5	0.1455716	0.0265978	0.1052878	0.1761556
NEEDPRO1	5	0.6563719	0.0547733	0.5993062	0.7329860

AGE=0.67 TMT=C

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	5	79.3900000	44.8776565	43.9900000	156.2000000
STEMM	5	15.1200000	8.2495160	9.6100000	24.7600000
BRANCHM	5	8.4820000	6.8221859	3.5600000	19.4900000
NEEDLM	5	55.7900000	32.2591080	30.8200000	111.9500000
STEMPRO1	5	0.2000651	0.0272121	0.1585147	0.2213094
BRCHPRO1	5	0.0974215	0.0207475	0.0720466	0.1344287
NEEDPRO1	5	0.7025468	0.0380231	0.6442619	0.7418330

AGE=0.67 TMT=D

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	5	36.3640000	13.9254544	18.6300000	49.4e 0000
STEMM	5	8.0880000	3.6328391	2.6600000	10.7700000
BRANCHM	5	3.1940000	2.0342148	0.8000000	5.1900000
NEEDLM	5	25.0640000	8.8125478	13.1700000	33.7800000
STEMPRO1	5	0.2151957	0.0386794	0.1599519	0.2690482
BRCHPRO1	5	0.0795132	0.0317405	0.0429846	0.1096677
NEEDPRO1	5	0.7053627	0.0647938	0.6212840	0.7919423

AGE=0.67 TMT=E

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	5	30.4640000	14.6053733	14.6700000	53.7400000
STEMM	5	8.0900000	4.3843301	3.2900000	14.2600000
BRANCHM	5	2.0840000	1.7133972	0.4100000	4.8000000
NEEDLM	5	20.2920000	8.7740680	10.9700000	34.6900000
STEMPRO1	5	0.2588886	0.0447582	0.2076057	0.3208283
BRCHPRO1	5	0.0596425	0.0247955	0.0279482	0.0893199
NEEDPRO1	5	0.6815237	0.0611868	0.6008403	0.7477846

1991

Tmt	Variable	N	Mean	Std Dev	Std Error
Contr.	PCOARSE	4	1575.81	1026.08	513.00
	PFINE	4	9.58	6.66	3.33
	PTOTAL	4	1595.39	1031.26	515.63
	STOTAL	0	0	0	0
A	PCOARSE	4	898.63	196.88	99.40
	PFINE	4	16.22	2.47	1.23
	PTOTAL	4	914.85	197.59	98.79
	STOTAL	4	25.64	12.01	6.01
B	PCOARSE	4	696.20	387.84	193.92
	PFINE	4	15.76	6.77	3.38
	PTOTAL	4	701.96	393.52	196.76
	STOTAL	4	79.07	41.01	20.50
C	PCOARSE	4	782.19	809.42	404.71
	PFINE	4	16.05	5.26	2.63
	PTOTAL	4	798.24	809.44	404.72
	STOTAL	4	108.71	23.85	11.93
D	PCOARSE	4	672.40	345.27	172.63
	PFINE	4	23.22	8.86	4.43
	PTOTAL	4	695.62	353.60	176.80
	STOTAL	4	183.78	93.43	46.71
E	PCOARSE	4	146.28	183.81	91.91
	PFINE	4	9.86	3.25	1.62
	PTOTAL	4	156.13	182.36	91.18
	STOTAL	4	254.56	105.53	52.76

Appendix 5. Sample size (N), means, standard deviations and errors for course, fine and total root mass (g m^{-2}) for *P.patula* (P) and total root mass (g m^{-2}) for *S. megaphylla* (S) for the three sampling periods.

1989

Tmt	Variable	N	Mean	Std Dev	Std Error
Contr.	PCOARSE	4	26.56	22.54	11.27
	PFINE	4	2.32	0.51	0.26
	PTOTAL	4	38.88	22.27	11.13
	STOTAL	4	0	0	0
A	PCOARSE	4	6.08	3.19	1.59
	PFINE	4	1.09	1.17	0.59
	PTOTAL	4	8.17	4.33	2.16
	STOTAL	4	17.23	9.40	4.70
B	PCOARSE	4	11.13	12.29	6.14
	PFINE	4	0.97	1.03	0.51
	PTOTAL	4	12.10	11.78	5.89
	STOTAL	4	17.35	7.53	3.76
C	PCOARSE	4	12.00	11.28	5.64
	PFINE	4	1.01	0.89	0.44
	PTOTAL	4	13.60	11.81	5.90
	STOTAL	4	33.71	15.53	6.77
D	PCOARSE	4	23.33	22.68	11.34
	PFINE	4	3.68	2.54	1.27
	PTOTAL	4	26.07	23.00	11.50
	STOTAL	4	34.46	10.17	5.09
E	PCOARSE	4	9.79	4.79	2.40
	PFINE	4	4.92	2.31	1.16
	PTOTAL	4	14.72	6.79	3.40
	STOTAL	4	58.61	19.06	9.53

1990

Tmt	Variable	N	Mean	Std Dev	Std Error
Contr.	PCOARSE	4	229.93	102.26	81.13
	PFINE	4	3.93	3.14	1.57
	PTOTAL	4	227.86	161.22	80.61
	STOTAL	0	0	0	0
A	PCOARSE	4	237.13	160.73	
	PFINE	4	6.34	3.34	
	PTOTAL	4	243.46	159.81	79.91
	STOTAL	4	26.89	7.81	3.90
B	PCOARSE	4	81.23	66.75	33.38
	PFINE	4	4.32	1.34	0.67
	PTOTAL	4	85.55	67.78	33.89
	STOTAL	4	46.79	10.82	5.41
C	PCOARSE	4	186.25	95.03	47.52
	PFINE	4	5.98	3.78	1.88
	PTOTAL	4	142.23	94.41	47.20
	STOTAL	4	72.89	23.57	11.78
D	PCOARSE	4	107.26	102.62	51.31
	PFINE	4	4.32	1.79	0.90
	PTOTAL	4	111.58	104.07	52.03
	STOTAL	4	138.47	78.83	39.42
E	PCOARSE	4	18.12	21.51	10.76
	PFINE	4	4.23	1.08	0.54
	PTOTAL	4	22.35	21.55	10.77
	STOTAL	4	163.65	55.02	27.51

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1991

Trat	Variable	N	Mean	Std Dev	Std Error
Contr.	PCOARSE	4	1394.45	484.54	242.27
	PFINE	4	718.91	278.26	139.13
	PTOTAL	4	2113.36	748.82	374.41
	STOTAL	0	0	0	0
A	PCOARSE	4	989.74	250.96	125.48
	PFINE	4	569.47	108.09	54.05
	PTOTAL	4	1559.21	310.68	155.34
	STOTAL	4	1026.05	403.72	201.86
B	PCOARSE	4	989.64	448.99	224.49
	PFINE	4	550.38	239.90	119.95
	PTOTAL	4	1540.02	666.08	333.04
	STOTAL	4	2596.61	1116.24	558.12
C	PCOARSE	4	699.28	212.62	106.31
	PFINE	4	545.90	208.55	104.28
	PTOTAL	4	1245.18	243.36	121.68
	STOTAL	4	3694.40	654.65	327.33
D	PCOARSE	4	946.47	234.48	117.24
	PFINE	4	702.30	306.23	153.11
	PTOTAL	4	1648.77	508.40	254.20
	STOTAL	4	6848.05	3307.42	1653.71
E	PCOARSE	4	361.13	85.36	42.68
	PFINE	4	361.86	107.32	53.66
	PTOTAL	4	722.99	67.88	33.94
	STOTAL	4	6785.17	3180.70	1590.35

Appendix 4. Sample size (N), means, standard deviations and errors for course, fine and total root density (m m^{-1}) for *P.patula* (P) and total root density (m m^{-3}) for *S. megaphylla* (S) for the three sampling periods.

1989

Tmt	Variable	N	Mean	Std Dev	Std Error
Contr.	PCOARSE	4	74.87	34.20	17.10
	PFINE	4	65.47	12.83	6.42
	PTOTAL	4	140.34	24.04	12.02
	STOTAL	4	0	0	0
A	PCOARSE	4	24.48	7.58	3.79
	PFINE	4	31.88	28.14	14.07
	PTOTAL	4	56.36	33.84	16.92
	STOTAL	4	727.33	273.99	136.99
B	PCOARSE	4	33.88	15.06	7.53
	PFINE	4	27.61	24.07	12.04
	PTOTAL	4	61.49	30.95	15.47
	STOTAL	4	1031.79	223.87	111.94
C	PCOARSE	4	50.10	40.92	20.46
	PFINE	4	42.70	32.16	16.08
	PTOTAL	4	92.80	65.51	32.76
	STOTAL	4	1206.43	456.25	228.12
D	PCOARSE	4	72.68	13.88	6.94
	PFINE	4	118.09	89.94	44.97
	PTOTAL	4	191.87	103.19	51.59
	STOTAL	4	1461.78	303.21	151.61
E	PCOARSE	4	58.93	30.85	15.43
	PFINE	4	143.76	69.74	34.87
	PTOTAL	4	202.69	99.01	49.51
	STOTAL	4	1865.44	338.00	169.00

1990

Tmt	Variable	N	Mean	Std Dev	Std Error
Contr.	PCOARSE	4	148.11	24.43	12.21
	PFINE	4	163.78	100.89	50.45
	PTOTAL	4	311.90	119.22	59.61
	STOTAL	0	.	0	0
A	PCOARSE	4	166.15	64.62	32.31
	PFINE	4	257.22	157.45	78.73
	PTOTAL	4	423.37	156.92	78.46
	STOTAL	4	1671.75	563.09	281.55
B	PCOARSE	4	155.67	100.68	50.34
	PFINE	4	166.70	76.14	38.07
	PTOTAL	4	322.45	176.85	88.28
	STOTAL	4	2793.98	1122.09	561.04
C	PCOARSE	4	102.69	56.02	28.01
	PFINE	4	207.09	147.90	73.95
	PTOTAL	4	309.78	184.51	92.25
	STOTAL	4	3942.22	865.27	432.64
D	PCOARSE	4	102.87	28.85	14.42
	PFINE	4	199.26	76.19	38.10
	PTOTAL	4	302.12	101.86	50.92
	STOTAL	4	5525.00	1704.21	852.10
E	PCOARSE	4	68.41	30.66	15.33
	PFINE	4	154.32	71.51	35.75
	PTOTAL	4	212.72	79.74	39.87
	STOTAL	4	6137.27	1343.09	671.54

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	19.12.91	100	0.085322	0.040814	0.004081
	06.07.92	99	0.13421	0.064963	0.006529
	14.06.93	99	0.27252	0.139035	0.013974
D	31.10.88	99	7.05E-07	6.01E-07	6.04E-08
	05.12.88	97	1.04E-06	8.82E-07	8.92E-08
	09.01.89	97	2.26E-06	2.02E-06	2.05E-07
	14.02.89	97	1.01E-05	8.21E-06	8.33E-07
	28.03.89	97	3.15E-05	2.22E-05	2.26E-06
	15.05.89	97	6.96E-05	5.63E-05	5.72E-06
	17.07.89	97	0.000172	0.000132	1.34E-05
	15.09.89	97	0.000275	0.000219	2.22E-05
	20.02.90	98	0.001864	0.001405	0.000142
	11.06.90	97	0.004701	0.003236	0.000329
	22.10.90	97	0.008656	0.005776	0.000587
	16.01.91	97	0.014552	0.009018	0.000916
	23.05.91	97	0.03292	0.021643	0.002198
	19.12.91	97	0.059613	0.037508	0.003808
	06.07.92	96	0.09999	0.061518	0.006279
	14.06.93	96	0.21329	0.127032	0.012965
E	31.10.88	100	7.36E-07	5.32E-07	5.32E-08
	05.12.88	100	1.09E-06	6.72E-07	6.75E-08
	09.01.89	100	2.02E-06	1.35E-06	1.35E-07
	14.02.89	100	8.39E-06	6.89E-06	5.89E-07
	28.03.89	100	2.22E-05	1.6E-05	1.6E-06
	15.05.89	100	4.76E-05	3.76E-05	3.76E-06
	17.07.89	100	8.77E-05	7.73E-05	7.73E-06
	15.09.89	100	0.000114	0.000116	1.16E-05
	20.02.90	98	0.000471	0.000489	4.94E-05
	11.06.90	95	0.001103	0.001138	0.000117
	22.10.90	92	0.002362	0.002326	0.000242
	16.01.91	91	0.004727	0.004307	0.000451
	23.05.91	90	0.013217	0.011112	0.001165
	19.12.91	90	0.032704	0.022922	0.002458
	06.07.92	87	0.06927	0.042658	0.004573
	14.06.93	97	0.18932	0.104989	0.011321

Appendix 3. Sample size (N), means (m^3 per tree), standard deviations and errors for volume index for *P. patula*.

Tmt	Date	N	Mean	Std Dev	Std Error
Contr.	31.10.88	100	6.73E-07	5.3E-07	5.3E-08
	05.12.88	97	1.08E-06	7.07E-07	7.18E-08
	09.01.89	94	1.95E-06	1.7E-06	1.75E-07
	14.02.89	93	9.37E-06	5.74E-06	5.95E-07
	28.03.89	93	3.21E-05	1.71E-05	1.77E-06
	15.05.89	92	9.28E-05	4.91E-05	5.12E-06
	17.07.89	92	0.000279	0.000138	1.44E-05
	15.09.89	92	0.000639	0.00033	3.44E-05
	20.02.90	99	0.005134	0.002473	0.000249
	11.06.90	99	0.012466	0.00544	0.000547
	22.10.90	99	0.023227	0.009797	0.000985
	16.01.91	99	0.034618	0.012704	0.001277
	23.05.91	99	0.084669	0.033276	0.003344
	19.12.91	99	0.145733	0.054685	0.005496
	06.07.92	97	0.21921	0.075867	0.007703
	14.06.93	94	0.3906	0.13749	0.014181
A	31.10.88	99	5.48E-07	4.29E-07	4.31E-08
	05.12.88	99	9.81E-07	8.24E-07	8.28E-08
	09.01.89	98	2.27E-06	1.99E-06	2.01E-07
	14.02.89	93	1.15E-05	9.14E-06	9.47E-07
	28.03.89	95	3.59E-05	2.87E-05	2.94E-06
	15.05.89	94	9.38E-05	7.87E-05	8.12E-06
	17.07.89	95	0.00026	0.000204	2.1E-05
	15.09.89	95	0.00055	0.000384	3.94E-05
	20.02.90	98	0.004548	0.00257	0.00026
	11.06.90	98	0.010804	0.00511	0.000516
	22.10.90	98	0.020951	0.008692	0.000878
	16.01.91	98	0.031313	0.011658	0.001179
	23.05.91	98	0.077272	0.031501	0.003182
	19.12.91	98	0.132536	0.051924	0.005245
	06.07.92	98	0.18319	0.069269	0.006997
	14.06.93	97	0.35218	0.128458	0.013043
B	31.10.88	100	6.17E-07	4.02E-07	4.02E-08
	05.12.88	99	1.03E-06	7.41E-07	7.45E-08
	09.01.89	98	2.1E-06	1.76E-06	1.77E-07
	14.02.89	97	7.78E-06	5.44E-06	5.52E-07
	28.03.89	98	2.44E-05	1.77E-05	1.79E-06
	15.05.89	98	6.24E-05	4.46E-05	4.51E-06
	17.07.89	98	0.000148	0.000105	1.06E-05
	15.09.89	98	0.000287	0.000214	2.16E-05
	20.02.90	100	0.002408	0.001453	0.000145
	11.06.90	100	0.006744	0.00383	0.000383
	22.10.90	100	0.014048	0.007029	0.000703
	16.01.91	100	0.022857	0.010347	0.001035
	23.05.91	99	0.055347	0.025909	0.002604
	19.12.91	98	0.097122	0.041934	0.004236
	06.07.92	97	0.15604	0.067866	0.006891
	14.06.93	96	0.30195	0.127558	0.013019
C	31.10.88	100	6.75E-07	4.78E-07	4.78E-08
	05.12.88	99	9.66E-07	6.39E-07	6.43E-08
	09.01.89	97	1.97E-06	1.62E-06	1.65E-07
	14.02.89	96	8.06E-06	5.7E-06	5.81E-07
	28.03.89	96	2.73E-05	2.35E-05	2.4E-06
	15.05.89	96	5.92E-05	4.47E-05	4.56E-06
	17.07.89	96	0.000142	0.000113	1.15E-05
	15.09.89	97	0.00026	0.000201	2.04E-05
	20.02.90	100	0.002087	0.001434	0.000143
	11.06.90	100	0.005801	0.003597	0.00036
	22.10.90	100	0.011464	0.006618	0.000662
	16.01.91	100	0.019284	0.010003	0.001
	23.05.91	100	0.046486	0.025419	0.002542

	06.07.92	99	6.45	1.19	0.12
	14.06.93	99	8.65	1.37	0.14
D	31.10.88	99	0.0952	0.0417	0.00419
	05.12.88	97	0.1249	0.04672	0.00474
	09.01.89	97	0.1742	0.05292	0.00537
	14.02.89	97	0.2607	0.08303	0.00843
	28.03.89	97	0.3743	0.12643	0.01284
	15.05.89	97	0.4868	0.17663	0.01793
	17.07.89	97	0.6196	0.20563	0.02088
	15.09.89	97	0.7624	0.24439	0.02481
	20.02.90	97	1.5934	0.47337	0.04782
	11.06.90	97	2.037	0.5395	0.0548
	22.10.90	97	2.285	0.6485	0.0658
	16.01.91	97	2.858	0.7293	0.074
	23.05.91	97	3.675	0.8595	0.0873
	19.12.91	97	4.569	1.0944	0.1111
	06.07.92	96	5.67	1.31	0.13
	14.06.93	96	7.89	1.82	0.17
E	31.10.88	100	0.1034	0.03585	0.00359
	05.12.88	99	0.1202	0.04025	0.00405
	09.01.89	100	0.1628	0.04517	0.00452
	14.02.89	100	0.2489	0.07052	0.00705
	28.03.89	100	0.3602	0.12598	0.0126
	15.05.89	100	0.5202	0.18858	0.01886
	17.07.89	100	0.666	0.26394	0.02639
	15.09.89	100	0.7398	0.2942	0.02942
	20.02.90	98	1.3647	0.41313	0.04173
	11.06.90	95	1.728	0.5499	0.0564
	22.10.90	92	2.028	0.5943	0.062
	16.01.91	91	2.386	0.7242	0.0759
	23.05.91	91	3.048	0.9319	0.0977
	19.12.91	87	4.127	1.026	0.11
	06.07.92	87	5.39	1.2	0.13
	14.06.93	86	7.74	1.38	0.15

Appendix 2. Sample size (N), means (m), standard deviations and errors for height of *P. patula*.

Tmt	Date	N	Mean	Std Dev	Std Error
Contr.	31.10.88	100	0.0922	0.04084	0.00408
	05.12.88	97	0.1177	0.0407	0.00413
	09.01.89	94	0.163	0.04111	0.00424
	14.02.89	93	0.2363	0.05723	0.00593
	28.03.89	93	0.3411	0.09117	0.00945
	15.05.89	92	0.4784	0.13775	0.01436
	17.07.89	92	0.6865	0.18377	0.01916
	15.09.89	92	0.9777	0.25022	0.02609
	20.02.90	99	2.0075	0.49483	0.04973
	11.06.90	99	2.74	0.5694	0.0572
	22.10.90	99	3.371	0.6685	0.0672
	16.01.91	99	4.033	0.7498	0.0754
	23.05.91	99	5.0146	0.9373	0.0942
	19.12.91	99	6.351	1.1095	0.1115
	06.07.92	97	7.8	1.13	0.11
	14.06.93	94	10.03	1.23	0.13
A	31.10.88	99	0.0875	0.03659	0.00368
	05.12.88	99	0.1172	0.04465	0.00449
	09.01.89	98	0.1699	0.04674	0.00472
	14.02.89	93	0.2589	0.07498	0.00777
	28.03.89	95	0.3641	0.11451	0.01175
	15.05.89	94	0.4957	0.15199	0.01568
	17.07.89	95	0.6883	0.20839	0.02138
	15.09.89	95	0.9126	0.25487	0.02615
	20.02.90	98	1.9386	0.4553	0.04609
	11.06.90	98	2.634	0.5432	0.0549
	22.10.90	98	3.292	0.6424	0.0649
	16.01.91	98	3.978	0.693	0.07
	23.05.91	98	5.027	0.8252	0.0834
	19.12.91	98	6.345	1.0204	0.1031
	06.07.92	98	7.36	1.28	0.13
	14.06.93	97	9.83	1.04	0.11
B	31.10.88	100	0.1006	0.03862	0.00386
	05.12.88	99	0.1191	0.04118	0.00414
	09.01.89	98	0.1624	0.03923	0.00396
	14.02.89	97	0.2406	0.06799	0.0069
	28.03.89	98	0.3281	0.10629	0.01074
	15.05.89	98	0.4301	0.14231	0.01438
	17.07.89	98	0.5841	0.17859	0.01804
	15.09.89	98	0.7406	0.22095	0.02232
	20.02.90	100	1.6028	0.41526	0.04153
	11.06.90	100	2.219	0.5699	0.057
	22.10.90	100	2.744	0.6854	0.0685
	16.01.91	100	3.436	0.7481	0.0748
	23.05.91	99	4.383	0.9239	0.0929
	19.12.91	98	5.607	1.0221	0.1033
	06.07.92	98	6.83	1.26	0.13
	14.06.93	97	9.08	1.54	0.16
C	31.10.88	100	0.0933	0.03753	0.00375
	05.12.88	99	0.1165	0.04132	0.00415
	09.01.89	97	0.1608	0.05119	0.0052
	14.02.89	96	0.2422	0.08295	0.00847
	28.03.89	96	0.3404	0.11656	0.0119
	15.05.89	96	0.4396	0.16029	0.01636
	17.07.89	96	0.6641	0.20501	0.02092
	15.09.89	97	0.7275	0.2305	0.02433
	20.02.90	100	1.6189	0.3966	0.03966
	11.06.90	100	2.176	0.5185	0.0518
	22.10.90	100	2.572	0.5995	0.0599
	16.01.91	100	3.203	0.6943	0.0694
	23.05.91	100	4.141	0.8195	0.0819
	19.12.91	100	5.205	0.9825	0.0982

	16.01.91	100	73.4	16.31	1.63
	23.05.91	100	100.2	22.56	2.26
	19.12.91	100	123.0	24.28	2.43
	06.07.92	100	138.0	27.60	2.80
	14.06.93	100	169.0	37.10	3.70
D	31.10.88	99	2.5	0.60	0.06
	05.12.88	97	2.7	0.54	0.05
	09.01.89	97	3.4	1.12	0.11
	14.02.89	97	5.7	1.46	0.15
	28.03.89	97	8.4	2.13	0.22
	15.05.89	97	10.8	3.04	0.31
	17.07.89	97	15.1	4.18	0.42
	15.09.89	97	16.9	5.24	0.53
	20.02.90	97	30.6	9.84	0.99
	11.06.90	97	44.0	12.56	1.27
	22.10.90	97	56.8	15.96	1.62
	16.01.91	97	66.0	17.38	1.76
	23.05.91	97	87.5	23.76	2.41
	19.12.91	97	105.6	28.44	2.89
	06.07.92	96	123.0	32.40	3.30
	14.06.93	96	153.0	41.20	4.20
E	31 10.88	100	2.6	0.51	0.05
	05.12.88	100	2.8	0.64	0.06
	09.01.89	100	3.3	0.98	0.10
	14.02.89	100	5.4	1.41	0.14
	28.03.89	100	7.2	1.77	0.18
	15.05.89	100	8.6	2.55	0.26
	17.07.89	100	10.1	3.25	0.33
	15.09.89	100	10.6	3.84	0.38
	20.02.90	98	15.8	6.79	0.69
	11.06.90	95	21.2	9.24	0.95
	22.10.90	92	29.5	11.64	1.21
	16.01.91	91	38.4	14.89	1.56
	23.05.91	91	57.7	20.70	2.17
	19.12.91	87	81.5	23.13	2.48
	06.07.92	87	106.0	26.30	2.80
	14.06.93	87	148.0	34.00	3.60

7. APPENDICES

Appendix 1. Sample size (N), means (mm), standard deviations and errors for root collar diameter.

Tmt	Date	N	Mean	Std Dev	Std Error
Contr.	31.10.88	100	2.5	0.59	0.06
	05.12.88	97	2.9	0.54	0.06
	09.01.89	94	3.2	1.10	0.11
	14.02.89	93	6.0	1.24	0.13
	28.03.89	93	9.3	1.92	0.20
	15.05.89	92	13.2	2.93	0.31
	17.07.89	92	19.1	4.18	0.44
	15.09.89	92	24.1	5.88	0.61
	20.02.90	99	48.1	9.77	0.98
	11.06.90	99	64.9	12.10	1.22
	22.10.90	99	80.3	13.53	1.36
	16.01.91	99	90.3	13.06	1.31
	23.05.91	99	125.9	20.69	2.08
	19.12.91	99	146.7	27.27	2.74
	06.07.92	98	163.0	24.80	2.50
	14.06.93	97	193.0	28.00	2.80
A	31.10.88	99	2.4	0.54	0.05
	05.12.88	99	2.7	0.60	0.06
	09.01.89	98	3.3	1.10	0.11
	14.02.89	93	6.1	1.62	0.17
	28.03.89	95	9.2	[illegible].22	0.23
	15.05.89	94	12.6	3.23	0.33
	17.07.89	95	18.2	4.65	0.48
	15.09.89	95	22.8	5.25	0.54
	20.02.90	98	46.2	9.70	0.98
	11.06.90	98	61.8	10.62	1.07
	22.10.90	98	77.4	11.65	1.18
	16.01.91	98	86.6	12.43	1.26
	23.05.91	98	120.5	19.63	1.98
	19.12.91	98	140.8	21.54	2.18
	06.07.92	98	151.0	23.00	2.30
	14.06.93	97	186.0	26.90	2.70
B	31.10.88	100	2.4	0.42	0.04
	05.12.88	99	2.8	0.57	0.06
	09.01.89	98	3.3	1.01	0.10
	14.02.89	97	5.4	1.26	0.13
	28.03.89	98	8.1	1.91	0.19
	15.05.89	98	11.2	2.60	0.26	
	17.07.89	98	15.0	[illegible]73	0.38
	15.09.89	98	18.0		0.50
	20.02.90	100	36.0		0.93
	11.06.90	100	51.3		1.24
	22.10.90	100	67.8	[illegible]	1.46
	16.01.91	100	77.8	[illegible]5.93	1.59
	23.05.91	99	107.2	2.43	2.25
	19.12.91	98	126.8	24.60	2.49
	06.07.92	97	145.0	26.10	2.60
	14.06.93	97	175.0	31.70	3.20
C	31.10.88	100	2.8	0.53	0.05
	05.12.88	99	2.7	0.53	0.05
	09.01.89	97	3.2	1.00	0.10
	14.02.89	96	5.3	1.39	0.14
	28.03.89	96	8.0	2.62	0.27
	15.05.89	96	10.5	2.87	0.29
	17.07.89	96	14.2	4.13	0.42
	15.09.89	97	17.0	4.98	0.51
	20.02.90	100	32.9	9.96	1.00
	11.06.90	100	47.8	12.82	1.28
	22.10.90	100	62.5	15.10	1.51

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0.67 years

I/J	A	B	C	D	F	K
A	.	0.6174	0.1464	0.0101	0.0096	0.0502
B	0.6174	.	0.3363	0.0352	0.0338	0.1398
C	0.1464	0.3363	.	0.2403	0.2337	0.6001
D	0.0101	0.0352	0.2403	.	0.9864	0.5125
E	0.0096	0.0338	0.2337	0.9864	.	0.5017
K	0.0502	0.1398	0.6001	0.5125	0.5017	.

1.76 years

I/J	A	B	C	D	E	K
A	.	0.0020	0.6305	0.0002	0.0001	0.3454
B	0.0020	.	0.0079	0.4377	0.0123	0.0261
C	0.6305	0.0079	.	0.0008	0.0001	0.6419
D	0.0002	0.4377	0.0008	.	0.0769	0.0033
E	0.0001	0.0123	0.0001	0.0769	.	0.0001
K	0.3454	0.0261	0.6419	0.0033	0.0001	.

2.72 years

I/J	A	B	C	D	E	K
A	.	0.1053	0.4605	0.3778	0.0001	0.3607
B	0.1053	.	0.0201	0.0139	0.0001	0.0128
C	0.4605	0.0201	.	0.8846	0.0006	0.8592
D	0.3778	0.0139	0.8846	.	0.0010	0.9742
E	0.0001	0.0001	0.0006	0.0010	.	0.0011
K	0.3607	0.0128	0.8592	0.9742	0.0011	.

Needles [Pr > |T| H0: LSMEAN(I)=LSMEAN(J)]

0.67 years

I/J	A	B	C	D	E	K
A	.	0.8067	0.8953	0.0001	0.0001	0.0001
B	0.8067	.	0.9099	0.0001	0.0001	0.0001
C	0.8953	0.9099	.	0.0001	0.0001	0.0001
D	0.0001	0.0001	0.0001	.	0.3915	0.0686
E	0.0001	0.0001	0.0001	0.3915	.	0.3256
K	0.0001	0.0001	0.0001	0.0686	0.3256	.

1.76 years

I/J	A	B	C	D	E	K
A	.	0.0353	0.8904	0.0455	0.0034	0.3390
B	0.0353	.	0.0254	0.0001	0.0001	0.0028
C	0.8904	0.0254	.	0.0616	0.0051	0.4124
D	0.0455	0.0001	0.0616	.	0.3189	0.2849
E	0.0034	0.0001	0.0051	0.3189	.	0.0414
K	0.3390	0.0028	0.4124	0.2849	0.0414	.

2.72 years

I/J	A	B	C	D	E	K
A	.	0.0781	0.7617	0.3815	0.0323	0.4044
B	0.0781	.	0.1420	0.3659	0.6913	0.0108
C	0.7617	0.1420	.	0.5601	0.0640	0.2570
D	0.3815	0.3659	0.5601	.	0.1951	0.0903
E	0.0323	0.6913	0.0640	0.1951	.	0.0036
K	0.4044	0.0108	0.2570	0.0903	0.0036	.

Appendix 9. The probability values for η_{stem}, η_{branch}, and η_{needle} 0.67, 1.76 and 2.72 years after establishment.

Stem [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

0.67 years

i/j	A	B	C	D	E	K
A	.	0.8040	0.1835	0.0001	0.0001	0.0001
B	0.8040	.	0.4131	0.0001	0.0001	0.0001
C	0.1835	0.4131	.	0.0001	0.0001	0.0001
D	0.0001	0.0001	0.0001	.	0.2340	0.0101
E	0.0001	0.0001	0.0001	0.2340	.	0.1511
K	0.0001	0.0001	0.0001	0.0101	0.1511	.

1.76 years

i/j	A	B	C	D	E	K
A	.	0.9402	0.5000	0.0001	0.0001	0.2555
B	0.9402	.	0.5486	0.0001	0.0001	0.2877
C	0.5000	0.5486	.	0.0001	0.0003	0.6404
D	0.0001	0.0001	0.0001	.	0.7969	0.0007
E	0.0001	0.0001	0.0003	0.7969	.	0.0015
K	0.2555	0.2877	0.6404	0.0007	0.0015	.

2.72 years

i/j	A	B	C	D	E	K
A	.	0.0141	0.3454	0.6910	0.0137	0.5624
B	0.0141	.	0.1200	0.0374	0.9914	0.0029
C	0.3454	0.1200	.	0.5833	0.1175	0.1304
D	0.6910	0.0374	0.5833	.	0.0365	0.3300
E	0.0137	0.9914	0.1175	0.0365	.	0.0028
K	0.5624	0.0029	0.1304	0.3300	0.0028	.

Stem [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

0.67 years

i/j	A	B	C	D	E	K
A	.	0.8643	0.9545	0.0018	0.0201	0.0288
B	.8643	.	0.8197	0.0009	0.0130	0.0180
C	0.9545	0.8197	.	0.0019	0.0232	0.0330
D	0.0018	0.0009	0.0019	.	0.3587	0.2877
E	0.0201	0.0130	0.0232	0.3587	.	0.8831
K	0.0288	0.0180	0.0330	0.2877	0.8831	.

1.76 years

i/j	A	B	C	D	E	K
A	.	0.1519	0.7570	0.6859	0.0001	0.4316
B	0.1519	.	0.0831	0.3130	0.0004	0.5119
C	0.7570	0.0831	.	0.4593	0.0002	0.2746
D	0.6859	0.3130	0.4593	.	0.0001	0.7218
E	0.0001	0.0004	0.0001	0.0001	.	0.0001
K	0.4316	0.5119	0.2746	0.7218	0.0001	.

2.72 years

i/j	A	B	C	D	E	K
A	.	0.5780	0.0189	0.4668	0.0001	0.1146
B	0.5780	.	0.0042	0.2014	0.0001	0.0347
C	0.0189	0.0042	.	0.0979	0.0001	0.4197
D	0.4668	0.2014	0.0979	.	0.0001	0.3884
E	0.0001	0.0001	0.0001	0.0001	.	0.0001
K	0.1146	0.0347	0.4197	0.3884	0.0001	.

Branches [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

AGE=2.72 TMT=C

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	19957.89	3745.18	15332.72	24471.56
ROOTM	4	4894.39	326.7913070	4476.76	5275.57
STEMM	4	4527.18	1302.04	3433.94	6383.81
BRANCHM	4	5266.52	2135.68	2465.67	7536.40
NEEDLM	4	5269.80	807.9689955	4520.76	6009.92
ROOTPRO2	4	0.2496674	0.0317905	0.2155796	0.2918743
STEMPRO2	4	0.2267141	0.0417960	0.1682030	0.2608665
BRCHPRO2	4	0.2551945	0.0668425	0.1808110	0.3080474
NEEDPRO2	4	0.2684240	0.0373253	0.2155061	0.2948440

AGE=2.72 TMT=D

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	11971.99	2195.85	8883.96	13915.69
ROOTM	4	3176.26	191.1409603	2984.96	3415.92
STEMM	4	2237.32	311.3980459	1951.83	2631.10
BRANCHM	4	3107.83	1258.06	1327.30	4289.66
NEEDLM	4	3448.58	920.3503458	2619.87	4356.62
ROOTPRO2	4	0.2714371	0.0447666	0.2329759	0.3359943
STEMPRO2	4	0.1907878	0.0354227	0.1456981	0.2197027
BRCHPRO2	4	0.2504872	0.0703452	0.1494041	0.3082807
NEEDPRO2	4	0.2872880	0.0316028	0.2412986	0.3130653

AGE=2.72 TMT=E

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	3433.96	824.5281258	2527.68	3960.20
ROOTM	4	626.9800000	24.2995679	592.3100000	647.7200000
STEMM	4	1166.92	220.9720892	958.9800000	1402.01
BRANCHM	4	490.4825000	206.4576503	258.6800000	757.3600000
NEEDLM	4	1149.58	355.8904917	677.8300000	1531.23
ROOTPRO2	4	0.1869805	0.0324000	0.1612359	0.2343110
STEMPRO2	4	0.3442503	0.0605679	0.2644419	0.3952126
BRCHPRO2	4	0.1386438	0.0382513	0.1023308	0.1912400
NEEDPRO2	4	0.3301155	0.0653021	0.2681417	0.4222417

AGE=2.72 TMT=K

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	26220.72	3568.09	21788.04	30422.83
ROOTM	4	8029.08	224.3668881	7786.11	8329.86
STEMM	4	5517.39	1033.48	3998.40	6301.61
BRANCHM	4	6647.71	1898.28	4287.04	8908.18
NEEDLM	4	6034.64	901.2130415	5006.63	7212.92
ROOTPRO2	4	0.3101954	0.0401519	0.2630249	0.3573871
STEMPRO2	4	0.2093528	0.0191633	0.1834217	0.2271819
BRCHPRO2	4	0.2494381	0.0366131	0.1967612	0.2927486
NEEDPRO2	4	0.2310134	0.0269072	0.1971395	0.2624596

AGE=1.76 TMT=D

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	2621.79	392.1797178	2252.16	3176.80
ROOTM	4	1178.14	64.0096851	1128.73	1267.78
STEMM	4	396.4125000	66.9072873	307.0200000	465.8100000
BRANCHM	4	385.7800000	118.6455713	290.5500000	542.9100000
NEEDLM	4	681.4575000	159.4529978	518.9900000	899.3100000
ROOTPRO2	4	0.4540478	0.0432863	0.3992002	0.5042271
STEMPRO2	4	0.1510822	0.0123850	0.1363225	0.1650558
BRCHPRO2	4	0.1372217	0.0225922	0.1239947	0.1709522
NEEDPRO2	4	0.2576703	0.0231779	0.2304410	0.2831759

AGE=1.76 TMT=E

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	608.5500000	69.1127591	526.9200000	692.3200000
ROOTM	4	267.0400000	11.9016245	253.8700000	282.8100000
STEMM	4	152.9825000	15.3165975	138.0000000	170.3500000
BRANCHM	4	49.5000000	23.9442644	29.8000000	79.0300000
NEEDLM	4	138.2275000	33.8015546	104.8100000	177.2100000
ROOTPRO2	4	0.4438436	0.0466310	0.3838254	0.4817099
STEMPRO2	4	0.2522607	0.0198125	0.2277364	0.2733503
BRCHPRO2	4	0.0790781	0.0302412	0.0305513	0.1141524
NEEDPRO2	4	0.2248176	0.0315750	0.1963528	0.2559054

AGE=1.76 TMT=K

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	9181.61	1477.51	7468.44	11061.38
ROOTM	4	2814.05	97.5551057	2689.08	2911.08
STEMM	4	1468.31	373.1719593	1193.74	2018.53
BRANCHM	4	2199.00	611.6570727	1342.57	2782.68
NEEDLM	4	2700.26	540.9322618	2143.66	3393.85
ROOTPRO2	4	0.3122048	0.0490903	0.2591877	0.3733671
STEMPRO2	4	0.1587076	0.0171908	0.1445566	0.1825423
BRCHPRO2	4	0.2361454	0.0377647	0.1797658	0.2600207
NEEDPRO2	4	0.2929424	0.0161789	0.2727398	0.3067560

AGE=2.72 TMT=A

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	26556.12	5337.57	20499.72	31151.79
ROOTM	4	7498.47	883.7758853	6436.06	8598.30
STEMM	4	4738.83	1892.02	2436.66	6398.29
BRANCHM	4	7390.63	1435.47	5472.59	8815.55
NEEDLM	4	6928.19	2016.14	4844.62	9513.85
ROOTPRO2	4	0.2872033	0.0378106	0.2376252	0.3191623
STEMPRO2	4	0.1751365	0.0483633	0.1031397	0.2068186
BRCHPRO2	4	0.2791937	0.0210112	0.2587601	0.3081012
NEEDPRO2	4	0.2584664	0.0373517	0.2205899	0.3053968

AGE=2.72 TMT=B

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	15754.96	1873.04	14092.26	18382.47
ROOTM	4	2930.11	90.0730376	2852.51	3030.25
STEMM	4	2557.75	887.5473551	1368.33	3381.64
BRANCHM	4	5236.18	1477.32	3210.15	6501.81
NEEDLM	4	5010.94	866.9084040	4102.08	6139.36
ROOTPRO2	4	0.1874169	0.0185155	0.1654765	0.2060585
STEMPRO2	4	0.1631850	0.0605867	0.0923005	0.2399573
BRCHPRO2	4	0.3333270	0.0860990	0.2277953	0.4385786
NEEDPRO2	4	0.3170710	0.0270863	0.2787052	0.3330435

AGE=0.67 TMT=E

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	5	145.4220000	32.5430610	110.3200000	196.5100000
ROOTM	5	114.9560000	17.9735536	95.6500000	142.7700000
STEMM	5	8.0900000	4.3843301	3.2900000	14.2600000
BRANCHM	5	2.0840000	1.7139972	0.4100000	4.8000000
NEEDLM	5	20.2920000	8.7740680	10.9700000	34.6900000
ROOTPRO2	5	0.7994280	0.0506486	0.7265279	0.8670232
STEMPRO2	5	0.0527449	0.0184991	0.0298223	0.0725663
BRCHPRO2	5	0.0129148	0.0080008	0.0037165	0.0244262
NEEDPRO2	5	0.1349095	0.0277216	0.0994380	0.1765305

AGE=0.67 TMT=K

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	5	372.0540000	32.8203067	328.1400	407.2800000
ROOTM	5	280.0780000	58.2808306	184.7800000	331.5500000
STEMM	5	20.6700000	5.6845316	13.5000000	27.5100000
BRANCHM	5	11.6840000	7.2115900	2.9000000	22.4600000
NEEDLM	5	59.6200000	26.2165339	28.4000000	98.4400000
ROOTPRO2	5	0.7480928	0.1181470	0.5631133	0.8809619
STEMPRO2	5	0.0555678	0.0143845	0.0358709	0.0891536
BRCHPRO2	5	0.0324474	0.0225754	0.0077056	0.0684464
NEEDPRO2	5	0.1638870	0.0840071	0.0754617	0.2999939

AGE=1.75 TMT=A

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	6131.13	466.3229188	5475.02	6658.48
ROOTM	4	1633.55	77.3876588	1528.73	1703.25
STEMM	4	868.2800000	100.1373387	780.0200000	1010.70
BRANCHM	4	1646.97	404.2377096	1208.46	2173.70
NEEDLM	4	1982.33	219.4975311	1723.65	2244.67
ROOTPRO2	4	0.2668909	0.0083639	0.2604055	0.2791732
STEMPRO2	4	0.1417803	0.0141903	0.1269512	0.1567981
BRCHPRO2	4	0.2668700	0.0520066	0.2206862	0.3365663
NEEDPRO2	4	0.3244495	0.0390784	0.2669126	0.3495303

AGE=1.75 TMT=B

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	3080.71	237.0101802	2865.29	3415.89
ROOTM	4	829.2800000	44.6419801	790.3300000	884.8300000
STEMM	4	528.4350000	75.5575253	427.7400000	597.0000000
BRANCHM	4	515.4175000	362.8950833	0	851.8500000
NEEDLM	4	1209.57	162.8919536	1074.53	1422.43
ROOTPRO2	4	0.2698651	0.0170732	0.2590375	0.2952092
STEMPRO2	4	0.1728067	0.0353101	0.1252207	0.2083559
BRCHPRO2	4	0.1624633	0.1107641	0	0.2494079
NEEDPRO2	4	0.3946642	0.0680478	0.3515085	0.4264349

AGE=1.75 TMT=C

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	4	3382.73	234.5402482	3202.69	3718.78
ROOTM	4	990.6600000	114.7696589	830.2300000	1081.63
STEMM	4	457.0775000	63.6224711	374.3900000	517.2600000
BRANCHM	4	861.8150000	128.6276047	690.6400000	990.7100000
NEEDLM	4	1082.28	121.7182759	974.6300000	[illegible]
ROOTPRO2	4	0.2938758	0.0379178	0.2466496	[illegible]
STEMPRO2	4	0.1351481	0.0137415	0.1154303	[illegible]
BRCHPRO2	4	0.2512487	0.0282665	0.2136437	0.2800523
NEEDPRO2	4	0.3199269	0.0269899	0.3004038	0.3533805

Appendix 8. Sample size (N), means, standard deviations and minimum and maximum values for w_{stem}, w_{branch}, and w_{needle} and η_{stem}, η_{branch}, and η_{needle}.

AGE=0.67 TMT=A

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	5	165.1320000	71.4645354	58.9300000	222.1700000
ROOTM	5	79.2140000	40.7305681	23.7500000	128.3600000
STEMM	5	15.1160000	5.7126246	8.0800000	21.1100000
BRANCHM	5	15.5840000	9.5060418	4.6900000	25.5400000
NEEDLM	5	55.2180000	20.9727685	22.4100000	74.6600000
ROOTPRO2	5	0.4640727	0.0665579	0.4030205	0.5777558
STEMPRO2	5	0.0963854	0.0253983	0.0658758	0.1371118
BRCHPRO2	5	0.0902006	0.0278332	0.0654092	0.1241674
NEEDPRO2	5	0.3473413	0.0538120	0.2621416	0.3997410

AGE=0.67 TMT=B

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	5	186.7260000	12.2375010	170.2700000	200.5100000
ROOTM	5	89.5280000	17.2108896	81.2700000	102.7400000
STEMM	5	19.1360000	5.4920879	13.8400000	25.6700000
BRANCHM	5	14.1660000	4.4614437	9.0000000	21.2400000
NEEDLM	5	63.8940000	15.3889804	42.4700000	88.5700000
ROOTPRO2	5	0.4824805	0.1038877	0.3133374	0.5832501
STEMPRO2	5	0.1016662	0.0239166	0.0735310	0.1280235
BRCHPRO2	5	0.0756889	0.0219439	0.0478154	0.1086223
NEEDPRO2	5	0.3401538	0.0748038	0.2494274	0.4529508

AGE=0.67 TMT=C

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	5	160.5780000	84.4253872	94.0100000	302.8000000
ROOTM	5	81.1880000	39.3720024	50.0300000	146.6000000
STEMM	5	15.1200000	6.2495160	9.6100000	24.7600000
BRANCHM	5	9.4820000	6.8221859	3.5600000	19.4900000
NEEDLM	5	55.7900000	32.2591080	30.8200000	111.9500000
ROOTPRO2	5	0.5115738	0.0202912	0.4841480	0.5321774
STEMPRO2	5	0.0973899	0.0007520	0.0817701	0.1054129
BRCHPRO2	5	0.0476796	0.0150984	0.0358572	0.0643659
NEEDPRO2	5	0.3433779	0.0282490	0.3068714	0.3735218

AGE=0.67 TMT=D

Variable	N	Mean	Std Dev	Minimum	Maximum
TOTALM	5	231.0860000	39.3444631	184.6200000	269.3700000
ROOTM	5	194.7220000	36.3640333	136.8900000	226.3900000
STEMM	5	8.0880000	3.0328391	2.6500000	10.7700000
BRANCHM	5	3.1940000	2.0342148	0.8000000	5.1900000
NEEDLM	5	25.0960000	8.8125478	13.1700000	33.7800000
ROOTPRO2	5	0.8418681	0.0635641	0.7879580	0.9318694
STEMPRO2	5	0.0352651	0.0139455	0.0190458	0.0450396
BRCHPRO2	5	0.0134077	0.0078528	0.0032919	0.0222413
NEEDPRO2	5	0.1096733	0.0346040	0.0541931	0.1447611

Needles [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

0.67 years

i/j	A	B	C	D	E	K
A	.	0.7670	0.0919	0.0770	0.2895	0.9076
B	0.7670	.	0.1621	0.1384	0.4437	0.6802
C	0.0919	0.1621	.	0.9315	0.5217	0.0723
D	0.0770	0.1384	0.9315	.	0.4677	0.0601
E	0.2895	0.4437	0.5217	0.4677	.	0.2406
K	0.9076	0.6802	0.0723	0.0601	0.2406	.

1.76 years

i/j	A	B	C	D	E	K
A	.	0.0081	0.7876	0.4299	0.2795	0.6616
B	0.0081	.	0.0164	0.0564	0.0003	0.0023
C	0.7876	0.0164	.	0.6021	0.1783	0.4802
D	0.4299	0.0564	0.6021	.	0.0641	0.2218
E	0.2795	0.0003	0.1783	0.0641	.	0.5172
K	0.6616	0.0023	0.4802	0.2218	0.5172	.

2.72 years

i/j	A	B	C	D	E	K
A	.	0.4459	0.9397	0.3633	0.2443	0.4791
B	0.4459	.	0.4024	0.8822	0.6843	0.1443
C	0.9397	0.4024	.	0.3251	0.2155	0.5271
D	0.3633	0.8822	0.3251	.	0.7959	0.1087
E	0.2443	0.6843	0.2155	0.7959	.	0.0639
K	0.4791	0.1443	0.5271	0.1087	0.0639	.

Appendix 7. The probability values for η_{stem}, η_{branch} and η_{needle} 0.67, 1.76 and 2.72 years after establishment.

Stem [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

0.67 years

I/J	A	B	C	D	E	K
1	.	0.6725	0.6263	0.3353	0.0214	0.0847
2	0.6725	.	0.9486	0.5867	0.0573	0.1891
3	0.6263	0.9486	.	0.6316	0.0659	0.2113
4	0.3353	0.5867	0.6316	.	0.1692	0.4375
5	0.0214	0.0573	0.0659	0.1692	.	0.5442
6	0.0847	0.1891	0.2113	0.4375	0.5442	.

1.76 years

I/J	A	B	C	D	E	K
A	.	0.2156	0.9544	0.0197	0.0001	0.2874
B	0.2156	.	0.1955	0.2568	0.0001	0.8593
C	0.9544	0.1955	.	0.0171	0.0001	0.2626
D	0.0197	0.2568	0.0171	.	0.0001	0.1909
E	0.0001	0.0001	0.0001	0.0001	.	0.0001
K	0.2874	0.8593	0.2626	0.1909	0.0001	.

2.72 years

I/J	A	B	C	D	E	K
A	.	0.2221	0.1024	0.5780	0.0001	0.0975
B	0.2221	.	0.0053	0.0780	0.0001	0.0050
C	0.1024	0.0053	.	0.2761	0.0009	0.9801
D	0.5780	0.0780	0.2761	.	0.0001	0.2654
E	0.0001	0.0001	0.0009	0.0001	.	0.0010
K	0.0975	0.0050	0.9801	0.2654	0.0010	.

Branches [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

0.67 years

I/J	A	B	C	D	E	K
A	.	0.5414	0.0826	0.0208	0.0051	0.1776
B	0.5414	.	0.2043	0.0834	0.0255	0.4561
C	0.0826	0.2043	.	0.6349	0.3180	0.5059
D	0.0208	0.0834	0.6349	.	0.5984	0.3183
E	0.0051	0.0255	0.3180	0.5984	.	0.1288
K	0.1776	0.4561	0.5059	0.3183	0.1288	.

1.76 years

I/J	A	B	C	D	E	K
A	.	0.0011	0.8521	0.0091	0.0001	0.0078
B	0.0011	.	0.0019	0.4862	0.0604	0.0050
C	0.8521	0.0019	.	0.0148	0.0001	0.7435
D	0.0091	0.4862	0.0148	.	0.0103	0.0332
E	0.0001	0.0604	0.0001	0.0103	.	0.0001
K	0.0078	0.0050	0.7435	0.0332	0.0001	.

2.72 years

I/J	A	B	C	D	E	K
A	.	0.7162	0.1813	0.2109	0.0001	0.4329
B	0.7162	.	0.0968	0.1084	0.0001	0.2527
C	0.1813	0.0968	.	0.9546	0.0002	0.5967
D	0.2109	0.1084	0.9546	.	0.0001	0.6366
E	0.0001	0.0001	0.0002	0.0001	.	0.0001
K	0.4329	0.2527	0.5967	0.6366	0.0001	.

Appendix 7. The probability values for η_{stem}, η_{branch} and η_{needle} 0.67, 1.76 and 2.72 years after establishment.

Stem [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

0.67 years

i/j	A	B	C	D	E	K
1	.	0.6725	0.6263	0.3353	0.0214	0.0847
2	0.6725	.	0.9486	0.5867	0.0573	0.1891
3	0.6263	0.9486	.	0.6316	0.0659	0.2113
4	0.3353	0.5867	0.6316	.	0.1692	0.4375
5	0.0214	0.0573	0.0659	0.1692	.	0.5442
6	0.0847	0.1891	0.2113	0.4375	0.5442	.

1.76 years

i/j	A	B	C	D	E	K
A	.	0.2156	0.9544	0.0197	0.0001	0.2874
B	0.2156	.	0.1955	0.2568	0.0001	0.8593
C	0.9544	0.1955	.	0.0171	0.0001	0.2626
D	0.0197	0.2568	0.0171	.	0.0001	0.1909
E	0.0001	0.0001	0.0001	0.0001	.	0.0001
K	0.2874	0.8593	0.2626	0.1909	0.0001	.

2.72 years

i/j	A	B	C	D	E	K
A	.	0.2221	0.1024	0.5780	0.0001	0.0975
B	0.2221	.	0.0053	0.0780	0.0001	0.0050
C	0.1024	0.0053	.	0.2761	0.0009	0.9801
D	0.5780	0.0780	0.2761	.	0.0001	0.2654
E	0.0001	0.0001	0.0009	0.0001	.	0.0010
K	0.0975	0.0050	0.9801	0.2654	0.0010	.

Branches [Pr > |T| H0: LSMEAN(i)=LSMEAN(j)]

0.67 years

i/j	A	B	C	D	E	K
A	.	0.5414	0.0626	0.0208	0.0051	0.1776
B	0.5414	.	0.2043	0.0834	0.0255	0.4561
C	0.0626	0.2043	.	0.6349	0.3180	0.5959
D	0.0208	0.0834	0.6349	.	0.5984	0.3163
E	0.0051	0.0255	0.3180	0.5984	.	0.1288
K	0.1776	0.4561	0.5959	0.3163	0.1288	.

1.76 years

i/j	A	B	C	D	E	K
A	.	0.0011	0.8521	0.0091	0.0001	0.6078
B	0.0011	.	0.0019	0.4662	0.0604	0.0050
C	0.8521	0.0019	.	0.0148	0.0001	0.7435
D	0.0091	0.4662	0.0148	.	0.0103	0.0332
E	0.0001	0.0604	0.0001	0.0103	.	0.0001
K	0.6078	0.0050	0.7435	0.0332	0.0001	.

2.72 years

i/j	A	B	C	D	E	K
A	.	0.7162	0.1913	0.2109	0.0001	0.4329
B	0.7162	.	0.0968	0.1084	0.0001	0.2527
C	0.1913	0.0968	.	0.9548	0.0002	0.5967
D	0.2109	0.1084	0.9548	.	0.0001	0.6366
E	0.0001	0.0001	0.0002	0.0001	.	0.0001
K	0.4329	0.2527	0.5967	0.6366	0.0001	.

AGE=2.72 TMT=K

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	18199.74	3501.18	14001.93	22420.72
STEMM	4	5517.39	1033.48	3996.40	6301.61
BRANCHM	4	6647.71	1898.28	4287.04	8906.18
NEEDLM	4	6034.64	901.2130415	5066.63	7212.92
STEMPROI	4	0.3036913	0.0256232	0.2810619	0.3361242
BRCHPROI	4	0.3660680	0.0385337	0.3061749	0.3972290
NEEDPROI	4	0.3362202	0.0502595	0.2916759	0.4084066

AGE=1.76 TMT=K

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	6387.57	1455.94	4679.97	8196.11
STEMM	4	1468.31	373.1719593	1193.74	2019.59
BRANCHM	4	2199.00	611.6570727	1342.57	2782.68
NEEDLM	4	2700.26	540.9322618	2143.66	3393.85
STEMPROI	4	0.2311472	0.0237917	0.2036516	0.2550743
BRCHPROI	4	0.3421352	0.0399206	0.2868758	0.3758350
NEEDPROI	4	0.4267175	0.0233574	0.4047103	0.4580499

AGE=2.72 TMT=A

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	19061.65	4708.36	14060.74	23749.34
STEMM	4	4738.83	1892.02	2438.66	6398.29
BRANCHM	4	7396.65	1435.47	5472.59	8815.55
NEEDLM	4	6926.19	2016.14	4644.62	9513.65
STEMPROI	4	0.2445940	0.0830927	0.1514894	0.2864225
BRCHPROI	4	0.3932128	0.0450606	0.3394132	0.4495949
NEEDPROI	4	0.3621930	0.0436214	0.3189451	0.4005859

AGE=2.72 TMT=B

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	12824.87	1792.74	11188.43	15322.22
STEMM	4	2557.75	887.5478551	1368.33	3381.54
BRANCHM	4	5256.16	1477.92	3210.15	6501.81
NEEDLM	4	5010.94	866.9084040	4102.08	6109.36
STEMPROI	4	0.2012884	0.0772724	0.1142921	0.3022354
BRCHPROI	4	0.4085349	0.1048424	0.2869159	0.5430747
NEEDPROI	4	0.3901765	0.0321272	0.3426332	0.4108467

AGE=2.72 TMT=C

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	15063.50	3420.10	10655.96	19196.99
STEMM	4	4527.18	1302.04	3433.94	6383.81
BRANCHM	4	5265.52	2135.68	2465.87	7538.40
NEEDLM	4	5269.80	607.9689855	4520.76	6009.92
STEMPROI	4	0.3028103	0.0567494	0.2216426	0.3564420
BRCHPROI	4	0.3377689	0.0776551	0.2271259	0.3927070
NEEDPROI	4	0.3594205	0.0611948	0.2747329	0.4164312

AGE=2.72 TMT=D

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	8793.74	2052.67	5899.00	10873.68
STEMM	4	2237.32	311.3980459	1951.83	2631.10
BRANCHM	4	3107.83	1259.06	1327.30	4289.66
NEEDLM	4	3448.68	820.3503424	2619.87	4356.52
STEMPROI	4	0.2542305	0.0612497	0.1899523	0.3308747
BRCHPROI	4	0.3401658	0.0796269	0.2250042	0.4018914
NEEDPROI	4	0.3956034	0.0509141	0.3238347	0.4441210

AGE=2.72 TMT=E

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	2806.99	602.2744015	1935.57	3321.72
STEMM	4	1166.92	220.9720892	958.9800000	1402.01
BRANCHM	4	490.4825000	206.4576593	258.6800000	757.3600000
NEEDLM	4	1149.58	355.8904917	877.8300000	1531.23
STEMPROI	4	0.4253190	0.0865705	0.3109704	0.5161529
BRCHPROI	4	0.1696024	0.0415778	0.1336454	0.2280024
NEEDPROI	4	0.4050786	0.0719040	0.3501966	0.5103056

AGE=0.67 TMT=K

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	5	91.9720000	37.2586603	44.9000000	143.3600000
STEMM	5	20.6700000	6.6845316	13.5000000	27.5100000
BRANCHM	5	11.6840000	7.2115900	2.9000000	22.4000000
NEEDLM	5	59.6200000	26.2166339	28.4000000	98.4400000
STEMPROI	5	0.2397385	0.0565745	0.1566685	0.3013393
BRCHPROI	5	0.1174268	0.0351172	0.0647321	0.1566685
NEEDPROI	5	0.6428611	0.0267522	0.6181561	0.6866629

AGE=1.76 TMT=A

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM		4497.58	384.1032055	3947.19	4767.33
STEMM	4	868.2800000	100.1373367	780.0200000	1010.70
BRANCHM	4	1546.97	404.2377096	1208.46	2173.70
NEEDLM	4	1982.33	219.4975311	1723.85	2244.87
STEMPROI	4	0.1934649	0.0199363	0.1725494	0.2120056
BRCHPROI	4	0.3637761	0.0691141	0.3061570	0.4571177
NEEDPROI	4	0.4427585	0.0550921	0.3625166	0.4848019

AGE=1.76 TMT=B

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	2251.43	212.4126033	2019.43	2531.06
STEMM	4	526.4350000	75.5575253	427.7400000	597.0000000
BRANCHM	4	515.4175000	362.8950833	0	851.9500000
NEEDLM	4	1209.57	182.8919536	1074.53	1422.43
STEMPROI	4	0.2373956	0.0527470	0.1589964	0.2956280
BRCHPROI	4	0.2199136	0.1497836	0	0.3365981
NEEDPROI	4	0.5426898	0.1082147	0.4752854	0.7043720

AGE=1.76 TMT=C

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	2392.07	245.5629257	2121.06	2654.08
STEMM	4	457.9775000	63.6224711	374.3900000	517.2600000
BRANCHM	4	851.8150000	128.9276047	690.6400000	990.7100000
NEEDLM	4	1082.28	121.7182759	974.6300000	1222.14
STEMPROI	4	0.1914477	0.0183231	0.1656538	0.2094142
BRCHPROI	4	0.3559229	0.0387375	0.3224150	0.4023878
NEEDPROI	4	0.4526284	0.0250384	0.4317585	0.4819544

AGE=1.76 TMT=D

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	1443.65	332.7187171	1115.56	1908.02
STEMM	4	396.4125000	66.9072873	307.0200000	465.8100000
BRANCHM	4	366.7800000	118.6455713	290.5500000	542.9100000
NEEDLM	4	681.4575000	159.4529978	518.3900000	899.3100000
STEMPROI	4	0.2775827	0.0261313	0.2441327	0.3072374
BRCHPROI	4	0.2506771	0.0289989	0.2271051	0.2845410
NEEDPROI	4	0.4717433	0.0121404	0.4618892	0.4889610

AGE=1.76 TMT=E

Variable	N	Mean	Std Dev	Minimum	Maximum
ABOVEM	4	340.7125000	66.7305459	273.0800000	426.5900000
STEMM	4	152.9625000	15.3165975	136.0000000	170.3500000
BRANCHM	4	49.5000000	23.9443641	29.8000000	79.0300000
NEEDLM	4	138.2275000	33.8015546	104.8100000	177.2100000
STEMPROI	4	0.4574174	0.0574503	0.3993296	0.5254165
BRCHPROI	4	0.1396 0	0 0423413	0.0971665	0.1852599
NEEDPROI	4	0.4029564	0.0271433	0.3774169	0.4351631

Appendix 16. Sample size (N), means (mg g^{-1}) and standard deviations for nitrogen, phosphorus, potassium, calcium and magnesium for *S. megaphylla* for January (1) and September (2), 1989.

Tmt	Nutrient	N	Mean	Std Dev
A	N1	4	3.13	0.09
	N2	4	3.22	0.11
	P1	4	0.20	0.02
	P2	4	0.21	0.02
	K1	4	3.35	0.74
	K2	4	4.32	1.18
	Ca1	4	0.22	0.05
	Ca2	4	0.30	0.03
	Mg1	4	0.26	0.06
	Mg2	4	0.32	0.14
B	N1	3	3.18	0.25
	N2	4	2.71	0.43
	P1	3	0.23	0.03
	P2	4	0.18	0.03
	K1	3	5.17	1.31
	K2	4	3.37	1.59
	Ca1	3	0.15	0.01
	Ca2	4	0.33	0.09
	Mg1	3	0.21	0.03
	Mg2	4	0.39	0.16
C	N1	3	2.64	0.70
	N2	4	2.86	0.30
	P1	4	0.20	0.10
	P2	4	0.19	0.04
	K1	4	4.74	3.14
	K2	4	2.90	1.63
	Ca1	4	0.22	0.06
	Ca2	4	0.33	0.02
	Mg1	4	0.29	0.15
	Mg2	4	0.39	0.10
D	N1	4	2.33	0.42
	N2	4	2.95	0.26
	P1	4	0.15	0.04
	P2	4	0.20	0.04
	K1	4	2.00	0.95
	K2	4	2.01	1.13
	Ca1	4	0.29	0.08
	Ca2	4	0.38	0.08
	Mg1	4	0.30	0.11
	Mg2	4	0.47	0.14
E	N1	4	1.95	0.25
	N2	4	2.07	0.30
	P1	4	0.10	0.03
	P2	4	0.14	0.03
	K1	4	1.95	0.79
	K2	4	2.03	0.89
	Ca1	4	0.22	0.04
	Ca2	4	0.33	0.09
	Mg1	4	0.18	0.04
	Mg2	4	0.25	0.07

Appendix 15. Sample size (N), means (mg g^{-1}) and standard deviations for nitrogen, phosphorus, potassium, calcium and magnesium for *P. patula* for Janur ...d September (2), 1989.

Tmt	Nutrient	N	Mean	Std Dev
Contr.	N1	4	1.75	0.08
	N2	4	1.37	0.11
	P1	4	0.12	0.01
	P2	4	0.10	0.0
	K1	4	0.41	0.02
	K2	4	0.46	0.07
	Ca1	4	0.19	0.02
	Ca2	4	0.24	0.06
	Mg1	4	0.08	0.01
	Mg2	4	0.08	0.01
A	N1	4	1.78	0.07
	N2	4	1.36	0.08
	P1	4	0.13	0.01
	P2	4	0.11	0.002
	K1	4	0.29	0.04
	K2	4	0.38	0.06
	Ca1	4	0.22	0.01
	Ca2	4	0.26	0.06
	Mg1	4	0.10	0.01
	Mg2	4	0.08	0.02
B	N1	4	1.72	0.09
	N2	4	1.40	0.12
	P1	4	0.14	0.01
	P2	4	0.13	0.03
	K1	4	0.27	0.06
	K2	4	0.34	0.05
	Ca1	4	0.19	0.01
	Ca2	4	0.24	0.04
	Mg1	4	0.09	0.01
	Mg2	4	0.08	0.13
C	N1	3	1.78	0.10
	N2	4	1.32	0.06
	P1	3	0.14	0.01
	P2	4	0.12	0.001
	K1	3	0.23	0.05
	K2	4	0.25	0.05
	Ca1	3	0.21	0.02
	Ca2	4	0.23	0.01
	Mg1	3	0.09	0.01
	Mg2	4	0.08	0.02
D	N1	4	1.56	0.09
	N2	4	1.37	0.09
	P1	4	0.15	0.04
	P2	4	0.12	0.004
	K1	4	0.29	0.14
	K2	4	0.18	0.53
	Ca1	4	0.24	0.11
	Ca2	4	0.27	0.03
	Mg1	4	0.11	0.05
	Mg2	4	0.10	0.007
E	N1	4	1.37	0.06
	N2	4	1.35	0.10
	P1	4	0.15	0.04
	P2	4	0.12	0
	K1	4	0.22	0.02
	K2	4	0.32	0.09
	Ca1	4	0.20	0.03
	Ca2	4	0.26	0.03
	Mg1	4	0.10	0
	Mg2	4	0.10	0.02

Appendix 14. Sample size (N), means (mg kg^{-1}) and standard deviations for soil nitrogen, phosphorus, potassium, calcium and magnesium for January (1) and September (2), 1989.

Tmt	Nutrient	N	Mean	Std Dev
Contr.	N1	4	1833.75	307.45
	N2	4	1979.50	595.62
	P1	4	8.18	1.33
	P2	4	22.00	6.06
	K1	4	71.17	12.18
	K2	4	46.50	5.20
	Ca1	4	369.12	139.96
	Ca2	4	440.25	170.61
	Mg1	4	91.38	24.78
	Mg2	4	47.25	23.94
A	N1	4	2065.75	357.75
	N2	4	1810.25	364.61
	P1	4	8.83	1.63
	P2	4	23.75	10.14
	K1	4	54.15	3.44
	K2	4	39.00	6.48
	Ca1	4	380.82	63.00
	Ca2	4	394.50	83.89
	Mg1	4	107.87	15.02
	MG2	4	41.00	9.66
B	N1	4	1843.25	346.12
	N2	4	1403.50	473.63
	P1	4	7.57	2.04
	P2	4	18.00	2.16
	K1	4	48.95	7.79
	K2	4	38.50	17.71
	Ca1	4	361.39	173.33
	Ca2	4	367.75	115.90
	Mg1	4	94.83	39.71
	Mg2	4	43.50	17.33
C	N1	4	1949.75	510.24
	N2	4	1844.75	770.26
	P1	4	7.35	1.09
	P2	4	16.25	4.99
	K1	4	64.16	24.21
	K2	4	36.25	15.41
	Ca1	4	359.92	203.22
	Ca2	4	388.50	222.74
	Mg1	4	96.84	26.75
	Mg2	4	44.75	25.20
D	N1	4	1843.25	375.39
	N2	4	1859.25	493.88
	P1	4	8.42	1.17
	P2	4	18.00	2.94
	K1	4	90.35	14.40
	K2	4	28.75	2.87
	Ca1	4	316.38	157.54
	Ca2	4	414.75	167.90
	Mg1	4	82.31	36.38
	Mg2	4	46.50	31.29
E	N1	4	2095.25	290.08
	N2	4	2085.00	294.00
	P1	4	10.22	4.11
	P2	4	14.50	1.91
	K1	4	57.38	8.50
	K2	4	46.50	10.08
	Ca1	4	440.42	66.78
	Ca2	4	484.25	72.12
	Mg1	4	109.69	17.01
	Mg2	4	67.75	11.62

Appendix 13. Example of dataset, (treatment C), for *P. patula* and *S. megaphylla* for the water balance study.

No.	Day	Month	Year	Pine	Pine	Pine root proportions for treatment C										Setaria	Setaria	Setaria root proportions for treatment C									
					height												height	LAI									
				(cm)		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	(cm)		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100
1	18	10	88	8.33	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.04	0.001	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
2	19	10	88	8.41	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.09	0.001	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
3	20	10	88	8.48	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.13	0.001	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
4	21	10	88	8.56	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.18	0.001	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
5	22	10	88	8.64	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.23	0.001	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
6	23	10	88	8.71	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.28	0.001	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
7	24	10	88	8.79	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.33	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
8	25	10	88	8.87	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.39	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
9	26	10	88	8.95	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.45	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
10	27	10	88	9.02	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.51	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
11	28	10	88	9.10	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.57	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
12	29	10	88	9.18	0.0008	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.63	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
13	30	10	88	9.33	0.0009	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.70	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
14	31	10	88	9.39	0.0009	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.77	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
15	1	11	88	9.46	0.0009	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.85	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
16	2	11	88	9.52	0.0009	0.59	0.31	0.06	0	0	0	0.04	0	0	0	1.93	0.002	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
17	3	11	88	9.59	0.0009	0.59	0.31	0.06	0	0	0	0.04	0	0	0	2.01	0.003	0.16	0.17	0.12	0.12	0.1	0.07	0.06	0.07	0.07	0.06
1070	24	9	91	473.51	2.5681	0.20	0.18	0.12	0.11	0.06	0.11	0.1	0.04	0.02	0.06	11.91	0.019	0.31	0.17	0.12	0.13	0.08	0.07	0.06	0.02	0.02	0.02
1071	25	9	91	474.19	2.5664	0.20	0.18	0.12	0.11	0.06	0.11	0.1	0.04	0.02	0.06	11.46	0.019	0.31	0.17	0.12	0.13	0.08	0.07	0.06	0.02	0.02	0.02
1072	26	9	91	474.87	2.5748	0.20	0.18	0.12	0.11	0.06	0.11	0.1	0.04	0.02	0.06	11.60	0.020	0.31	0.17	0.12	0.13	0.08	0.07	0.06	0.02	0.02	0.02
1073	27	9	91	475.55	2.5832	0.20	0.18	0.12	0.11	0.06	0.11	0.1	0.04	0.02	0.06	11.76	0.020	0.31	0.17	0.12	0.13	0.08	0.07	0.06	0.02	0.02	0.02
1074	28	9	91	476.24	2.5916	0.20	0.18	0.12	0.11	0.06	0.11	0.1	0.04	0.02	0.06	11.91	0.020	0.31	0.17	0.12	0.13	0.08	0.07	0.06	0.02	0.02	0.02
1075	29	9	91	476.92	2.6000	0.20	0.18	0.12	0.11	0.06	0.11	0.1	0.04	0.02	0.06	12.07	0.021	0.31	0.17	0.12	0.13	0.08	0.07	0.06	0.02	0.02	0.02
1076	30	9	91	477.60	2.6085	0.20	0.18	0.12	0.11	0.06	0.11	0.1	0.04	0.02	0.06	12.23	0.021	0.31	0.17	0.12	0.13	0.08	0.07	0.06	0.02	0.02	0.02

Appendix 12. Example of the dataset of climate variables and values for the water balance study (No = sample day, TMax = maximum daily temperatue, TMin = minimum daily temperature, Wind = wind velocity, Rnet = net radiation and VPD = vapour pressure deficit).

No	Day	Month	Year	Rain (mm)	TMax (°C)	TMax (°C)	Wind (m/s)	Rnet (MJ/day)	VPD (kPa)
1	18	10	88	24.7	17.4	15.4	1.21	15.69	1.071
2	19	10	88	24.4	15.7	13.4	1.2	15.69	1.063
3	20	10	88	23.6	16.1	12.9	1.2	15.69	1.055
4	21	10	88	0	19.2	13.6	1.2	15.69	1.047
5	22	10	88	18	27.7	14.3	1.2	15.69	1.039
6	23	10	88	0	19.4	12.1	1.19	15.69	1.031
7	24	10	88	3	21.6	10	1.19	15.69	1.023
8	25	10	88	0.5	17.7	0	1.19	15.69	1.015
9	26	10	88	6	15.1	0	1.18	15.69	1.007
10	27	10	88	0.3	17.1	10.4	1.18	15.69	0.999
11	28	10	88	0	24.5	11.5	1.18	15.69	0.991
12	29	10	88	3.7	31.6	15.5	1.17	15.69	0.983
13	30	10	88	1.4	15	11.5	1.17	15.69	0.975
14	31	10	88	0	25	11.7	1.17	15.69	0.967
15	1	11	88	2	28.4	14.2	1.17	15.69	0.959
16	2	11	88	0	27	14.9	1.16	15.69	0.951
17	3	11	88	1.5	28.5	15.9	1.16	15.69	0.943
18	4	11	88	0.9	17.7	11.6	1.16	15.69	0.935
19	5	11	88	1.9	23	13.2	1.15	15.69	0.927
20	6	11	88	0	22.2	15	1.15	15.69	0.919
21	7	11	88	0	25.7	14.4	1.15	15.69	0.911
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1055	9	9	91	0.2	20.1	13.4	1.21	8.01	1.222
1056	10	9	91	2.4	24.3	12	1.21	7.13	1.225
1057	11	9	91	0	17.9	12.8	1.21	4.40	1.227
1058	12	9	91	0	20.6	12	1.21	7.94	1.230
1059	13	9	91	1.2	26.6	13.4	1.2	1.70	1.233
1060	14	9	91	0	17.2	13.5	1.2	6.52	1.228
1061	15	9	91	0	24.7	13.4	1.2	5.26	1.223
1062	16	9	91	0	33.7	13	1.2	1.48	1.218
1063	17	9	91	0	24.8	9.9	1.2	7.01	1.213
1064	18	9	91	0	31.9	11.6	1.2	11.02	1.208
1065	19	9	91	0	31.2	15.9	1.2	10.09	1.203
1066	20	9	91	0	22	12.2	1.21	8.36	1.198
1067	21	9	91	0	24.3	14.5	1.21	7.79	1.193
1068	22	9	91	0.3	26.4	13	1.21	5.99	1.187
1069	23	9	91	0	29.3	12.5	1.21	7.07	1.182
1070	24	9	91	22.5	29.5	15.4	1.21	7.64	1.177
1071	25	9	91	7.3	16.6	13	1.21	8.57	1.172
1072	26	9	91	0	19.9	11.5	1.21	5.17	1.167
1073	27	9	91	0	25.3	11.4	1.21	3.38	1.162
1074	28	9	91	12.3	29.6	13.4	1.21	9.78	1.157
1075	29	9	91	3	21.3	13.9	1.21	5.37	1.152
1076	30	9	91	0	29.9	10.7	1.21	4.46	1.147

Appendix 12. Example of the dataset of climate variables and values for the water balance study (No = sample day, TMax = maximum daily temperatue, TMin = minimum daily temperature, Wind = wind velocity, Rnet = net radiation and VPD = vapour pressure deficit).

No	Day	Month	Year	Rain (mm)	TMax (°C)	TMax (°C)	Wind (m/s)	Rnet (MJ/day)	VPD (kPa)
1	18	10	88	24.7	17.4	15.4	1.21	15.69	1.071
2	19	10	88	24.4	15.7	13.4	1.2	15.69	1.063
3	20	10	88	23.6	16.1	12.9	1.2	15.69	1.055
4	21	10	88	0	19.2	13.6	1.2	15.69	1.047
5	22	10	88	18	27.7	14.3	1.2	15.69	1.039
6	23	10	88	0	19.4	12.1	1.19	15.69	1.031
7	24	10	88	3	21.6	10	1.19	15.69	1.023
8	25	10	88	0.5	17.7	0	1.19	15.69	1.015
9	26	10	88	6	15.1	0	1.18	15.69	1.007
10	27	10	88	0.3	17.1	10.4	1.18	15.69	0.999
11	28	10	88	0	24.5	11.5	1.18	15.69	0.991
12	29	10	88	3.7	31.5	15.5	1.17	15.69	0.983
13	30	10	88	1.4	15	11.5	1.17	15.69	0.975
14	31	10	88	0	25	11.7	1.17	15.69	0.967
15	1	11	88	2	28.4	14.2	1.17	15.69	0.959
16	2	11	88	0	27	14.9	1.16	15.69	0.951
17	3	11	88	1.5	28.5	15.9	1.16	15.69	0.943
18	4	11	88	0.9	17.7	11.6	1.16	15.69	0.935
19	5	11	88	1.9	23	13.2	1.15	15.69	0.927
20	6	11	88	0	22.2	15	1.15	15.69	0.919
21	7	11	88	0	25.7	14.4	1.15	15.69	0.911
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1055	9	9	91	0.2	20.1	13.4	1.21	8.01	1.222
1056	10	9	91	2.4	24.3	12	1.21	7.13	1.225
1057	11	9	91	0	17.9	12.8	1.21	4.40	1.22.
1058	12	9	91	0	20.6	12	1.21	7.94	1.230
1059	13	9	91	1.2	26.6	13.4	1.2	1.70	1.233
1060	14	9	91	0	17.2	13.5	1.2	.52	1.228
1061	15	9	91	0	24.7	13.4	1.2	.26	1.223
1062	16	9	91	0	33.7	13	1.2	1.48	1.218
1063	17	9	91	0	24.8	9.9	1.2	7.01	1.213
1064	18	9	91	0	31.9	11.6	1.2	11.02	1.208
1065	19	9	91	0	31.2	15.9	1.2	10.09	1.203
1066	20	9	91	0	22	12.2	1.21	8.36	1.198
1067	21	9	91	0	24.3	14.5	1.21	7.75	1.193
1068	22	9	91	0.3	26.4	13	1.21	5.99	1.187
1069	23	9	91	0	29.3	12.5	1.21	7.27	1.182
1070	24	9	91	22.5	29.5	15.4	1.21	7.64	1.177
1071	25	9	91	7.3	16.6	13	1.21	8 57	1.172
1072	26	9	91	0	19.9	11.5	1.21	5.17	1.167
1073	27	9	91	0	25.3	11.4	1.21	3.38	1.162
1074	28	9	91	12.3	29.6	13.4	1.21	9.78	1.157
1075	29	9	91	3	21.3	13.9	1.21	5.37	1.152
1076	30	9	91	0	20.9	10.7	1.21	4.46	1.147

Appendix 11. Sample size (N), means and standard deviations for pre-dawn plant water potential for *S. megaphylla*.

Tmt	Date	N	Mean	Std Dev
A	06/12	12	0.11	0.05
	12/01	12	0.02	0.04
	21/02	6	0.13	0.08
	29/03	12	0.12	0.04
	16/05	12	0.08	0.04
	18/07	12	0.29	0.07
	19/09	12	0.33	0.14
B	06/12	12	0.09	0.04
	12/01	12	0.03	0.05
	21/02	5	0.10	0
	29/03	12	0.17	0.09
	16/05	12	0.04	0.02
	18/07	12	0.28	0.09
	19/09	12	0.28	0.10
C	06/12	12	0.16	0.17
	12/01	12	0.03	0.04
	21/02	1	0.10	.
	29/03	12	0.10	0.04
	16/05	12	0.08	0.04
	18/07	12	0.20	0.06
	19/09	12	0.44	0.16
D	06/12	12	0.14	0.11
	12/01	12	0.05	0.06
	21/02	7	0.11	0.04
	29/03	12	0.14	0.06
	16/05	12	0.08	0.05
	18/07	12	0.44	0.29
	19/09	12	0.42	0.14
E	06/12	12	0.10	0.03
	12/01	11	0.06	0.07
	21/02	7	0.71	1.63
	29/03	12	0.15	0.09
	16/05	12	0.11	0.05
	18/07	12	0.51	0.28
	19/09	11	0.82	0.51

Appendix 10. Sample size (N), means, standard deviations and errors for pre-dawn plant water potential for *P.patula*.

Tmt	Date	N	Mean	Std Dev	Std Error
Contr.	06/12	12	0.33	0.09	0.02
	12/01	11	0.33	0.13	0.04
	21/02	12	0.26	0.13	0.04
	29/03	12	0.40	0.20	0.06
	16/05	12	0.35	0.10	0.03
	18/07	12	0.51	0.24	0.07
	19/09	12	0.56	0.31	0.09
A	06/12	12	0.32	0.11	0.03
	12/01	12	0.32	0.11	0.03
	21/02	12	0.26	0.07	0.02
	29/03	12	0.40	0.07	0.02
	16/05	12	0.37	0.08	0.02
	18/07	12	0.72	0.23	0.07
	19/09	11	0.47	0.21	0.06
B	06/12	12	0.33	0.11	0.03
	12/01	12	0.43	0.13	0.04
	21/02	12	0.29	0.10	0.03
	29/03	12	0.42	0.14	0.04
	16/05	12	0.38	0.13	0.04
	18/07	12	0.85	0.27	0.08
	19/09	12	0.73	0.21	0.06
C	06/12	12	0.39	0.19	0.05
	12/01	12	0.29	0.13	0.04
	21/02	12	0.27	0.17	0.05
	29/03	12	0.49	0.15	0.04
	16/05	12	0.49	0.10	0.03
	18/07	12	0.85	0.29	0.08
	19/09	12	0.75	0.30	0.09
D	06/12	12	0.33	0.09	0.03
	12/01	12	0.3.	0.12	0.03
	21/02	12	0.24	0.09	0.03
	29/03	12	0.41	0.10	0.03
	16/05	12	0.40	0.07	0.02
	18/07	12	0.81	0.41	0.12
	19/09	12	0.64	0.35	0.10
E	06/12	12	0.30	0.07	0.02
	12/[illegible]	11	0.36	0.12	0.04
	21/02	12	0.30	0.10	0.03
	29/03	12	0.39	0.11	0.03
	16/05	12	0.35	0.07	0.02
	18/07	12	0.94	0.31	0.09
	19/09	12	1.57	0.43	0.12