GROWTH AND NUTRIENT CYCLING IN CULTIVATED *PROTEA NERIIFOLIA* R.Br.

by

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Flowers of the Proteaceous shrub
Protea neriifolia R.Br.

DECLARATION

I hereby declare that the research work reported in this thesis is the result of my own investigation, except where acknowledged.

Rolf-Dieter Heinsohn

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ABSTRACT

The family Proteaceae is distributed predominantly in the south-western Cape Province of South Africa and south-western and south-eastern Australia, areas which fall within the climate term mediterranean ecosystems. A major characteristic of these areas is the low level of total nutrients in the soil, particularly nitrogen and phosphorus. In their natural habitat, therefore, Proteaceae occur on well-drained and highly leached soils of low nutrient status. Efficient nutrient cycling processes, combined with morphological adaptations designed to facilitate maximum absorption of available nutrients (for example, proteoid roots in the Proteaceae), conserve the limited nutrients available, allowing for the continued growth of these shrubs under conditions of low nutrient availability.

In recent years, flowers of certain species of Proteaceae have become popular as cut-flowers. As a result, many species of Proteaceae are currently cultivated worldwide, under conditions that match as closely as possible those found in mediterranean ecosystems. Traditionally, the shrubs are cultivated on nutrient poor soils and of concern is the loss of nutrients through the removal of flowers for commercial sale.

Therefore, the aim of the present study was to evaluate growth and mineral cycling in the proteaceaous shrub, *Protea neriifolia* R.Br., cultivated in a summer rainfall area in South Africa. Nutrient loss through flower removal and its effect on nutrient cycling was quantified. Optimum levels of ammonium nitrogen, phosphorus and potassium for the growth of *P. neriifolia* seedlings was determined and this formed the basis for the fertilization of mature *P. neriifolia* shrubs. The effects of inorganic fertilizers on growth and mineral cycling in mature *P. neriifolia* shrubs was monitored and the effectiveness of inorganic fertilizers, applied to redress nutrient loss, assessed.

The primary response of seedlings of *P. neriifolia* to applied ammonium nitrogen, phosphorus and potassium was to ammonium nitrogen, with increased growth with increasing levels of applied ammonium nitrogen, to a maximum of 7 mM applied as 60 ml per week. Seedling response to applied phosphorus and potassium became noticeable only at higher levels of ammonium nitrogen supply, and at these levels seedlings were observed to respond favourably to relatively high phosphorus (0.65 mM) and potassium (1.25 mM) levels, also

applied as 60 ml per week. Since nitrate nitrogen has been shown to be toxic to certain Proteaceae it was not tested in this investigation. However, results from the nursery trial suggested favourable *P. neriifolia* growth with a non-nitrate inorganic fertilizer with an NPK ratio of approximately 5:1:3 (mass basis) and this was used as a basis for testing the effects of inorganic fertilizers on growth and nutrient cycling in mature *P. neriifolia* shrubs.

Growth and nutrient cycling was monitored in mature *P. neriifolia* shrubs for four years: two years prior to the application of inorganic fertilizers and two years with the application of inorganic fertilizers, including unfertilized control shrubs. Two inorganic fertilizer preparations were tested. Both had as their base the commercial slow-release urea based fertilizer, Plantosan, which has an NPK ratio of 5:1:3. This was supplemented with either ammonium sulphate or urea at a rate of 80 g per running metre every three months.

Whole shrub dimensions showed similar growth of *P. neriifolia* shrubs cultivated in a summer rainfall area to the growth of the species in its natural habitat. Applied fertilizers did appear to increase growth, although these results became apparent only after 18 months. As recorded in other Proteaceae, the stem length of all shrubs decreased with increasing age of the shrubs although this decrease was less in shrubs receiving inorganic fertilizers. Branching did not appear to be affected by shrub age or the application of inorganic fertilizers. However, shrub reproductive productivity did increase with age, with greater increases in fertilized shrubs. Furthermore, flowers from fertilized shrubs were larger than those from unfertilized shrubs, although this phenomenon also only became apparent after 18 months. There was also a change in nutrient allocation patterns with those shrubs growing on soils of lowest nutrient availability directing more resources to root growth. This appeared to occur at the expense of stem material which, in each case, accounted for more than 50% of the total shrub biomass.

Although shrub age and the application of fertilizers did influence total shrub growth, the timing of growth events were not affected. They were, however, not synchronous to growth events in *P. neriifolia* growing in its natural habitat. Vegetative growth showed a peak in early spring (September) and the peak reproductive period was in autumn (March, April and May). Maximum litter production (comprising more than 90% leaf litter) occurred in late autumn to early summer (May to December) and this, too, was not affected by shrub age or the application of inorganic fertilizers. Proteoid root occurrence was greatest in late winter/spring (August to November), co-incident with peak above-ground vegetative growth.

There are two models that have been developed to describe the growth of overstorey shrubs in mediterranean ecosystems. In the first, the availability of nutrients is described as being of over-riding importance in determining growth events, while in the second model, soil moisture and temperature are regarded as primary growth determinants. Neither model could adequately explain the shift in phenophase observed in *P. neriifolia* cultivated in a summer rainfall area. However, soil moisture and temperature do appear more important in determining phenophase events, particularly since the application of inorganic fertilizers did not appear to alter the timing of these growth events. Nevertheless, the importance of nutrients cannot be ignored as growth can occur only provided sufficient nutrients are available.

Seasonal variations in nutrient concentrations of leaf, stem, floret and bract material were observed both prior to and after the application of inorganic fertilizers. However, of importance is that only shrubs receiving Plantosan plus ammonium sulphate retained comparable nutrient levels in tissue types compared with nutrient levels in the corresponding tissue types prior to the application of inorganic fertilizers. Shrubs receiving Plantosan plus urea and unfertilized shrubs had lower nutrient levels suggesting growth at the expense of previously absorbed nutrients. This was supported by a change in nutrient allocation patterns, particularly more nutrients in below-ground biomass in shrubs of the latter two treatments.

The cycling of nitrogen, phosphorus and potassium was measured prior to and after the application of inorganic fertilizers. During nutrient cycling, the amount of nitrogen circulated was larger than the amount of potassium which, in turn, was larger than the amount of phosphorus. Three nutrient pools, in the above- and below-ground biomass and the soil, were measured and these comprise the plant/soil system. Inputs into the plant/soil system measured were from rainfall and inorganic fertilizers. Nutrient flows within the plant/soil system measured were leaching, due to rainfall, from the shrub onto the soil, litter production and decomposition, and nutrient uptake by the shrubs, into above- and below-ground nutrient pools. Losses from the plant/soil system recorded in this study were losses from the soil through stream-water, and the largest loss, loss through the removal of flowers for commercial sale.

In the absence of flower harvesting the flow of nutrients in the plant/soil system, combined with inputs from rainfall, appeared adequate for the continued growth of the shrubs. However, in the presence of flower harvesting there appeared to be a nutrient budget deficit. This deficit appeared to worsen with increasing shrub age and increasing reproductive productivity in the absence of inorganic fertilizer applications. This was confirmed by nutrient depletion from the soil available nutrient pool. Although inorganic fertilizers did not dramatically alter soil total nutrient pools, soil levels of soluble nitrogen and available phosphorus did show slight increases but not in accordance with the levels of fertilizers applied. It is likely that a high proportion of the applied fertilizers was lost to the plant/soil system before becoming available to the system. This could have occurred through leaching through the soil profile although this was not measured in this study. Nevertheless, inorganic fertilizers did appear to compensate for nutrient loss through the removal of flowers for commercial sale, and the ammonium sulphate supplemented preparation resulted in the most favourable response.

Due to a number of cultivation practices which affected the growth of the *P. neriifolia* shrubs, results are not always strictly comparable with natural systems. However, a number of results obtained in this invegstigation do have horticultural implications and these are briefly discussed with regard to the cultivation of the Proteaceae, particularly *P. neriifolia* cultivation.

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1 INTRODUCTION

1.1 Natural distribution and habitat of the Proteaceae

The family Proteaceae which comprises 62 genera and approximately 1 400 species (Ferreira, 1986a) has evolved as a distinctly southern family (Johnson and Briggs, 1975) with two major distribution areas: the south-western Cape Province of South Africa (Goldblatt, 1978; Taylor, 1978; Kruger, 1979), and south-western and south-eastern Australia (Specht, 1979). Due to the climate both regions are considered to be 'mediterranean ecosystems' (Day, 1983) and are commonly termed 'fynbos' in the south-western Cape (Day, 1983; Kruger, Mitchell and Jarvis, 1983) and 'kwongan' in south-western Australia (Day, 1983; Beard and Pate, 1984). Within these two mediterranean ecosystems members of the Proteaceae are widespread (George, Hopkins and Marchant, 1979; Kruger, 1979; Lamont, Hopkins and Hnatiuk, 1984).

Mediterranean ecosystems correspond very closely with the winter rainfall regions of the world (Day, 1983) and have well defined seasons viz. a cool and wet winter season with rainfall between 250 - 1 200 mm and a hot and dry summer season when, despite high rainfall in winter, water can be growth limiting (Day, 1983; Specht and Moll, 1983). Although subjected to seasonal drought, the seasonal and annual water balance does permit a relatively long growing season, for example, 6 - 10 months in Australian kwongan (Prescott, Collins and Shirpurkar, 1952; Specht and Moll, 1983). Temperatures are seldom extreme and mean monthly minima and maxima range from 8 - 12° C and 18 - 30° C, respectively (Day, 1983). Frosts may occur in low lying inland regions and snow is common only on mountain tops (Day, 1983).

An additional similarity between mediterranean ecosystems throughout the world viz. the Cape fynbos, kwongan heath, chaparral (California, U.S.A.), matorral (Chile) and maquis (Mediterranean Basin), is that they are all characterised by low levels of total soil nutrients (Day, 1983). The Cape fynbos and Australian kwongan are considered to have considerably lower levels of total soil nutrients than counterparts elsewhere in the world (Christensen, 1973; De Bano and Conrad, 1978; Kruger, 1979; Specht, 1979; Low, 1980; Rundel and Parsons, 1980; Day, 1983; Low and Bristow, 1983; Milewski, 1983; Bettenay, 1984; Van Daalen, 1984). Day (1983) has characterized the soils of mediterranean ecosystems (based on nitrogen and phosphorus concentrations, and total exchangeable cations) into three groupings: nutrient poor and strongly leached (fynbos and kwongan), nutrient rich and moderately leached (chaparral, matorral, maquis and south-central Australian heath) and agriculturally rich and weakly leached (small areas of south central Australian heath and Californian chaparral).

1.2 Mineral nutrition of plants in mediterranean ecosystems, particularly the Proteaceae

Soils of mediterranean ecosystems vary widely (Day, 1983; Specht and Moll, 1983) and are characterised by low levels of plant nutrients, toxic levels of certain nutrients, cation imbalances and high or low pH (Specht and Moll, 1983). Specifically, fynbos and kwongan occur on nutrient poor and highly leached soils (Day, 1983). In accordance, good growth of Proteaceae in southern Africa and southern Australia has been observed on highly leached, well-drained soils of low pH (Vogts, 1958; Jeffrey, 1964; Moore, 1966; Hocking and Thomas, 1974; Vogts, 1977a; Vogts, 1977b; Vogts, 1982). Minerals in these soils are at a very low level or unavailable to plants (Specht and Moll, 1983): nitrogen and phosphorus tend to be in short supply but one or more nutrients (for example, potassium, sulphur, copper, zinc or molybdenum) may also be growth limiting (Specht and Moll, 1983).

Nitrogen and phosphorus are generally considered to be the nutrients that limit growth in mediterranean ecosystems (Specht and Moll, 1983). Consequently, nutrient studies have concentrated on these two minerals. Application of nitrogen has been shown to increase plant growth in chaparral (Helmers, Horton, Juhren and O'Keefe, 1955), and in Australian heath, phosphorus additions have resulted in improved growth (Specht, 1963). In combination, nitrogen and phosphorus have been shown to increase the growth of Australian heath (Specht, 1963; Jones, 1968; Heddle and Specht, 1975). These data support the earlier statement that in various ecosystems either nitrogen, phosphorus or nitrogen and phosphorus may be growth limiting. In southern African fynbos, increases in shoot extension and dry mass in response to nitrogen addition were found in first season growth of *Leucospermum parile*, while addition of phosphorus resulted in reduced shoot growth (Witkowski, Mitchell and Stock, 1990a). However, the addition of mineral nutrients did not appear to affect the timing or duration of shoot extension (Witkowski *et al.*, 1990a), the timing of the annual peak of litter production (Witkowski, 1989a), or the composition of the litter (Witkowski, 1989a). In contrast, bush morphology, for example, increased branching in *Leucospermum parile*, does exhibit plasticity with increased nutrient availability (Witkowski *et al.*, 1990a).

There is little known of the precise nutrient requirements of the Proteaceae (Parvin, Criley and Bullock, 1973; Groves and Keraitis, 1976; Thomas, 1979; Claassens, 1981; Thomas, 1980; Tibbits and Bachelard, 1981; Thomas, 1981) other than that they are sensitive to high levels of both nitrate and phosphorus (Claassens, 1981; Nichols and Beardsell, 1981; Vogts, 1982).

Although sensitive to high nitrate levels (Claassens, 1981), Proteaceae have exhibited increased growth in response to increased nitrogen availability, particularly ammonium nitrogen (Claassens, 1986). Nitrate nitrogen can be used by certain *Protea* species, for example, *Leucospermum pattersoni* and *Protea repens* but ammonium nitrogen is preferable (Claassens, 1986). Sensitivity to nitrate nitrogen (Lewis and Stock, 1978) has been demonstrated in *Leucadendron salignum* grown hydroponically (Heinsohn, 1983), and this sensitivity is possibly due to low levels of nitrate reductase in certain species of Proteaceae (Stock and Lewis, 1982).

High soil phosphorus is regarded as detrimental to the growth of Proteaceae (Thomas, 1974; Nichols and Beardsell, 1979; Claassens, 1981). Abundant supply of phosphorus has been linked to the death of *Banksia* species in western Australia (Ellyard and McIntyre, 1978) and to a reduction in yield of roots of *Leucospermum* species grown in sand culture (Claassens, 1981). Furthermore, Claassens (1986) reports that the phosphorus requirements of Proteaceae are low and that this is associated with low phosphorus levels in leaves when growth is 'normal'. In contrast, Prasad and Dennis (1986) found no indication of phosphorus toxicity in container or field grown *Leucadendron salignum* cv. Safari Sunset.

In the growth of Proteaceae, soil potassium levels do not appear to be critical (Claassens, 1981) except at high levels of available potassium where yield of *Leucospermum cordfolium* was shown to be detrimentally affected (Claassens and Foelscher, 1980). Furthermore, the importance of potassium to the growth of Proteaceae may lie in the finding that phosphorus toxicity of Proteaceae in their natural habitat was alleviated by high nitrogen and high potassium levels (Nichols and Beardsell, 1981).

1.3 Phenology and growth in mediterranean ecosystems

There exist two main models to explain plant growth in mediterranean ecosystems.

In mediterranean ecosystems a distinction is made between shrublands on relatively fertile soils (Specht, 1979; Specht and Moll, 1983) and heathlands on infertile soils (Specht, 1979). In the phenological model developed by Specht, Rogers and Hopkins (1981) and Specht, Moll, Pressinger and Sommerville (1983) nutrient availability is considered to be the major determinant of shoot development in mediterranean-type heathlands on strongly leached, nutrient poor soils. Shoot growth in heathland overstorey species occurs in late spring-summer at the expense of nutrients released from litter decomposing in spring. Leaf drop coincides with shoot growth, and it is implicit in the model that nutrient uptake occurs concurrently with shoot growth (Specht *et al.*, 1981; Specht *et al.*, 1983). The overstorey species of mediterranean shrublands growing on moderately leached, relatively fertile soils, are not subject to severe nutrient limitation and shoot growth occurs in spring, prior to leaf fall in the dry summer.

The model proposed by Kummerow (1983) describes similar timing of growth events as detailed in the model by Specht *et al.* (1981) and Specht *et al.* (1983) with most species of mediterranean shrublands showing growth flushes in spring and summer. Evidence for a spring growth pattern does exist for certain protea species (heathland vegetation), for example, *P. nitida, P. repens* and *P. neriifolia* (Kruger, 1981). However, unlike the model of Specht *et al.* (1981) and Specht *et al.* (1983) which suggests nutrient availability to be the major phenophase determinant, the model by Kummerow (1983) suggests temperature and soil moisture as the principle determinants of phenophases. It is proposed that vegetative growth flushes, fine root growth and litter fall are moisture driven while flowering and litter decomposition are temperature driven (Kummerow, 1983).

Data on the phenology of Proteaceae have shown shoot growth in late spring/early summer (November-December) and peak flowering in autumn/early winter (Mostert, Siegfried and Louw, 1980; Kruger, 1981; Pierce, 1984). Bond (1980) reported maximum growth for *Leucadendron ulignosum* and *P. repens* in summer, followed by peak flowering in *P. repens* in late summer-early autumn. A summer peak in litter production has been observed in a number of fynbos species (Bond, 1980; Pierce and Cowling, 1984b; Mitchell and Coley, 1987; Witkowski, 1989a). In contrast, Kruger (1981) has reported a principal leaf fall period in late summer-autumn.

Since growth periodicities are adaptations to seasonal stress on plant growth (Bond, 1980), it is important to note that within the limits of their natural distribution (winter rainfall areas) the Proteaceae appear to grow during the driest period of the year. According to the model proposed by Specht *et al.*, (1981) and Specht *et al.*, (1983) this summer growth is dependent on nutrient availability. According to Kummerow (1983) who predicts spring growth, water and temperature are growth phenophase determinants. It is probable that all three factors are important and that in any one season phenophases are determined by an optimum balance of soil moisture, nutrient availability, temperature and photoperiod suitable for growth.

1.4 Nutrient cycling and the role of fire in mediterranean ecosystems

A feature of mediterranean ecosystems is the low levels of available nutrients in the soil, particularly in the heathlands of the southern Cape (South Africa) and southern and western Australia (Day, 1983). As in other ecosystems, mineral cycling processes are operative in mediterranean heathlands, and three mineral flow pathways can be identified viz. geochemical, biogeochemical and biochemical cycling (Charley and Richards, 1983). The first links the external environment to the ecosystem, the second is the circulation of nutrient capital between soil, standing crop and litter subsystems, while the third includes nutrient redistributions in the living biomass that act to conserve elements within the standing crop (Charley and Richards, 1983). The relative importance of each varies from element to element, but all three pathways have been shown to operate in mediterranean ecosystems (Groves, 1983; Rundel, Bate, Low, Miller, Miller and Mitchell, 1983).

1.4.1 Linkage between the environment and the ecosystem

Major sources of nutrients to any system include hydrological input, weathering of rocks and biological fixation. Nutrient levels may be decreased by leaching, volatization and through the loss of particulate matter (Rundel *et al.*, 1983). Of concern in this investigation is the cycling of nitrogen, phosphorus and potassium.

Nitrogen inputs into mediterranean heathlands occur via hydrological input (primarily precipitation) and nitrogen fixation in the soil (Rundel *et al.*, 1983; Stock and Lewis, 1986a; Stock, Lewis and Allsopp, 1988), although data for the latter are limited in fynbos and kwongan (Rundel *et al.*, 1983). Phosphorus inputs from precipitation are thought to be low and the primary source of phosphorus to the soil is thought to be from weathering of the parent rock (Rundel *et al.*, 1983). This is also thought to be the case with the major cations, including potassium (Rundel *et al.*, 1983).

Nutrient loss through leaching is thought to be low because the low level of soil nutrients and the relatively low degree of precipitation in mediterranean heathlands would limit the amount of leaching (Rundel *et al.*, 1983). However, the amount of nutrient lost through runoff following fire can be considerable as shown for nitrogen and phosphorus in chaparral (De Bano and Conrad, 1978). An important aspect of fire regimes is the large amounts of nitrogen that can be lost through volatilization (De Bano *et al.*, 1979). Although volatilization of cations is thought to be low, high potassium losses have been reported in chaparral (De Bano and Conrad, 1978).

Mineral loss through particulate loss has not been quantified in mediterranean ecosystems but is thought to be restricted. Possibly the major impact of such nutrient loss would occur immediately following fire but to date no data are available (Rundel *et al.*, 1983).

1.4.2 Circulation of nutrient capital

Nutrient capital cycling between the plant, soil and litter has recently been shown to be important in mediterranean ecosystems in providing nutrients for plant growth, particularly during periods between fires (Schlesinger and Hasey, 1981). The rate of litter decomposition is important in determining nutrient release and availability to plants (Rundel *et al.*, 1983). Between fires there is slow decomposition during which phosphorus and potassium are released more quickly than nitrogen (Rundel *et al.*, 1983). These nutrients are then available for plant uptake from the soil.

However, due to the slow decomposition of leaf litter in mediterranean ecosystems (Schlesinger and Hasey, 1981; Specht, 1981; Mitchell and Coley, 1987) fire is important in consuming litter (Groves, 1983; Mitchell, 1983) thereby increasing the level of available nutrients such as nitrogen and phosphorus for plant growth (Groves, 1983). Fire may cause large losses of nutrients from the system (particularly nitrogen) but it is important in making soil nutrients available for uptake by plants (Mitchell, 1983). There is also evidence of luxury uptake of nutrients during the early post-fire phases of regeneration (Rundel, 1983).

An additional important nutrient capital cycling process involves mineral transformations (Rundel *et al.*, 1983). Possible nitrogen transformations include: ammonification, nitrification, immobilization and denitrification. These processes are thought to occur at low rates in mediterranean ecosystems (Lewis and Stock, 1978; Rundel *et. al.*, 1983).

Phosphorus transformations have been less studied. However, the mineralization of organic phosphates and the release of phosphate from insoluble inorganic phosphates occur as a result of the activity of soil bacteria, soil fungi, mycorrhizas, non-mycorrhizal root systems and proteoid roots (Rundel *et. al.*, 1983). Although there is little data available to quantify the relative importance of mineral transformations in mediterranean ecosystems, it is important to note that these transformations are dependent on such factors as soil pH, temperature and moisture (Rundel *et al.*, 1983).

1.4.3 Mineral redistribution

An aspect of nutrient cycling that has thus far received little attention in mediterranean ecosystems concerns the redistribution of minerals within the biotic component. However, there is evidence of efficient internal cycling of nitrogen and phosphorus by vegetation in mediterranean ecosystems (Read and Mitchell, 1983). An example of internal nutrient cycling is the translocation out of the leaf into storage tissues of significant amounts of nitrogen and phosphorus in chaparral evergreens prior to drought-induced abscission (Schlesinger and Hasey, 1981).

Therefore, in the absence of fire, a combination of external (litter) and internal (redistribution) nutrient cycling maximises nutrient availability for growth (Specht *et al.*, 1983).

1.5 Strategies to enhance nutrient absorption

An additional aspect of the mineral nutrition of plants in mediterranean ecosystems concerns plant adaptations to maximise nutrient uptake. Strategies may take one of two forms: an increase in efficiency of uptake, or tapping of novel sources of nutrients (Lamont, 1983a). An increase in uptake efficiency is usually associated with a specialized root system, for example, proteoid roots in the Proteaceae (Lamont, 1972; 1976; 1983a,b; 1986), dauciform (Cyperaceae), capillaroid (Restionaceae) or stalagmiform (Myrtaceae) (Lamont, 1983a). Fungal mycorrhizas are also important in the nutrition of some of the flora represented in mediterranean ecosystems (Lamont, 1983a).

Of importance in this discussion are the proteoid roots of the Proteaceae. These are dense clusters of rootlets (Purnell, 1960; Lamont, 1972; Lamont, 1983a) that greatly increase the absorptive root surface area (Lamont, 1983a; Lamont, 1986; Vorster and Jooste, 1986a,b) and may also act as temporary stores for absorbed nutrients (Vorster and Jooste, 1986b). In the mediterranean heathlands of the southern Cape Province and southern and western Australia, specialized roots are concentrated in the nutrient enriched litter layer (Lamont, 1983a; Specht, 1981). The close association between sites of nutrient release and absorption favours rapid uptake and minimizes nutrient escape (Lamont, 1983a).

The tapping of novel nutrient sources such as atmospheric nitrogen by nodules (Lamont, 1983a) or the preying on insects by carnivorous leaves (Lamont, 1983a) is important in some mediterranean ecosystems but not in the mineral nutrition of the Proteaceae.

1.6 The cultivation of Proteaceae

There are a number of species of the family Proteaceae whose flowers are important in the commercial cut-flower industry (Vogts, 1982; Davies, 1984). Historically flowers for sale were removed from plants growing in their natural habitat (wildflower picking) (Heinsohn and Pammenter, 1986) but more recently those species of commercial importance have been cultivated (Parvin, 1984). As described in Section 1.1, members of the family Proteaceae have a natural distribution within the southern Cape (South Africa) and southern and western Australian mediterranean heathlands. These gene pools form the basis for the commercial cultivation industry in Hawaii, California, Israel, New Zealand, Zimbabwe, Australia and South Africa (Cape and the Transvaal) (Parvin, 1984).

Although cultivation of Proteaceae is a world-wide phenomenon (Parvin, 1984), cultivation practices in most instances are similar. For example, proteas are cultivated on well-drained, nutrient poor soils of low pH which closely match the conditions under which proteas grow in their natural habitat. However, there are a number of problems associated with the cultivation of the Proteaceae, ranging from physiological, for example, the blackening of leaves in certain species (Whitehead and De Swardt, 1982; Brink and De Swardt, 1986; Ferreira, 1986b), seed germination (Brown, Van Staden and Jacobs, 1986; Mitchell, Van Staden and Brown, 1986; Rebelo and Rourke, 1986) and flower quality improvement (Jacobs, Napier and Malan, 1986; Napier, Malan, Jacobs and Bernitz, 1986) to horticultural, for example, plant propagation by tissue culture (Ben-Jaacov and Jacobs, 1986) or through the establishment of rooted cuttings (Brits, 1986) to pathological, for example, fungal problems associated with propagation material (Benic, 1986), fungal diseases in established protea orchards (Knox-Davies, Van Wyk and Marasas, 1986; Von Broembsen and Brits, 1986) and insect predation on mature protea shrubs (Coetzee, 1986).

Of concern to ecologists, physiologists and horticulturists is that both in the case of wildflower picking (Low and Lamont, 1986; Van Wilgen and Lamb, 1986) and the harvesting of cultivated flowers (Heinsohn and Pammenter, 1986) nutrient reserves are being depleted from systems already operating under extremely low nutrient availability (Low and Lamont, 1986). This is exacerbated in the cultivated system where, in the absence of fire, nutrient return to the soil is likely to be less rapid than in the natural state.

1.7 Aims of this study

Various species of the Proteaceae were cultivated for commerical flower production in the eastern Transvaal highveld of South Africa, a summer rainfall area. Except for summer rainfall, habitat (for example, nutrient poor soils) and growth conditions (for example, temperature) were similar to those found in mediterraean ecosystems and shrub growth was observed to closely match that of counterparts growing in their natural habitat.

The annual flower yield of five year old *Protea neriifolia*, cultivated at a density of 1 000 shrubs ha^{-1}, was 700 kg ha^{-1} (dry mass) (Heinsohn and Pammenter, 1986). The harvest of flowers represents a potentially large loss of nutrients from the system and the question arises as to whether shrub growth and flower production can be sustained without nutrient replacement.

Therefore, nutrient depletion as a result of flower harvesting formed the basis of the present study in which the growth, phenology, mineral status and mineral cycling of *P. neriifolia* cultivated in a summer rainfall area were investigated.

There were three primary aims to the present study:

- to monitor the growth, phenology and nutrient status, and to determine nutrient (nitrogen, phosphorus and potassium) budgets for cultivated *P. neriifolia* in order to quantify budget deficits due to the removal of flowers for sale.

- to determine the growth response of *P. neriifolia* seedlings to various combinations of applied nitrogen, phosphorus and potassium. The results of this nursery trial formed the basis for the selection of inorganic fertilizers that were used in field trials in attempts to correct budget deficits due to flower removal.

- to examine the effects of inorganic fertilizers on the growth, phenology, nutrient status and nitrogen, phosphorus and potassium budgets of cultivated *P. neriifolia*.

The results of this study are compared with data for Proteaceae (specifically *P. neriifolia*, where available) growing in their natural habitat and are interpreted in terms of existing information and models of mediterranean heathlands.

It is important to note that the study was not designed to provide definitive fertilizer recommendations for cultivated proteas. Rather, fertilizers were applied in attempts to replace nutrients depleted during flower removal.

2 MATERIALS AND METHODS

From the aims of the study presented in Section 1.7 it is evident that the work presented in this thesis can be incorporated in three main sections viz. the growth, phenology, nutrient status and nutrient budgets of *P. neriifolia* prior to the addition of inorganic fertilizers; the effects of N, P and K on the growth and chemical composition of *P. neriifolia* seedlings; and the growth, phenology, nutrient status and nutrient budgets of *P. neriifolia* with and without the addition of inorganic fertilizers.

Materials and methods prior to and after the addition of inorganic fertilizers are essentially the same and will be presented together. Where deviations occur or where particular measurements refer to one period only, this will be noted in the text. For clarity it is important to note here that field fertilization involved three treatments (inclusive of control plants) and where appropriate the replication within these three treatments is noted. The materials and methods used in the seedling trial will be presented separately.

The statistics used throughout the analysis of the results included the calculation of standard deviations, analysis of variance and the calculation of minimum significant differences (MSD) (Sokal and Rohlf, 1981). Differences in means that are greater than the MSD are significant at the levels stated. Deviations from this statistical treatment of data are noted in the appropriate places in the text.

2.1 Study plant and cultivation site

2.1.1 Study plant

Protea neriifolia R. Br. cv. Kouga (Figure 2.1) was selected as the study plant for this investigation. This is because it has been suggested that *P. neriifolia* will thrive under a variety of environmental conditions (Vogts, 1977a) thereby lending itself to cultivation (Vogts, 1977a). Evidence of this is the large-scale cultivation of *P. neriifolia* both in summer and winter rainfall areas (personal observation).

Figure 2.1 Five year old cultivated *Protea neriifolia* R.Br.

P. neriifolia has been described as a tree-like shrub which grows to a height of 3 m (Vogts, 1977a). Branching is uneven and the shrubs are non-symmetrical, although, in general, the shrubs have a spread equal to their height (Vogts, 1977a). The main stem is short and thick with lateral branching occurring at ground level (Rourke, 1980). The shrubs do not have a lignotuber. Rooting depth of the tap root is approximately 300 mm with between three and five major lateral roots spreading from the tap root (Vogts 1977a). Minor lateral roots branch from the major lateral roots and in the top 200 mm of soil these minor lateral roots terminate in dense clusters of tiny rootlets called proteoid roots (Lamont, 1986). Shoot extension and branching continues during each growth season and approximately 40-60% of the branches develop terminal inflorescences (Vogts, 1977a). Leaves are narrow and elongated with a prominent midrib. They measure from 100-180 mm in length and 14-35 mm in width (Vogts, 1977a; Rourke, 1980). Leaf colour varies from yellow-green to blue-green, occasionally with a red margin (Vogts, 1977a; 1982). Flowers are very variable ranging from pale, creamy green to soft pink or deep red always with contrasting bearded tips to the bracts (Vogts, 1977a; 1982). Average flower head size is 125 mm long and 75 mm wide (Vogts, 1977a). Within the flower head are the individual florets (250-400) each comprising both male and female flower parts (Vogts, 1977a). Approximately 15% of the ovaries develop mature seed (brown, nut-like fruits covered in golden-brown styliform hairs) measuring 9 by 3 mm (Vogts, 1977a). In the natural habitat, flowers remain on the shrubs for up to one year before seed dispersal and flower shedding (Vogts, 1982). Unlike in other species of Proteaceae, seed dispersal in *P. neriifolia* is not fire dependent (Rourke, 1980). Flowers of *P. neriifolia* are of great economic value and there are a number of variants which possess different qualities of commercial importance, for example, rich flower colour and good keeping quality once the flower has been cut (Vogts, 1977a).

2.1.2 Cultivation site

The growth and nutritional studies described in this report were conducted on *P. neriifolia* shrubs cultivated at Mount Sheba Nature Reserve (MSNR), Pilgrims Rest District, South Africa. MSNR ($24^{\circ}58^{I}$S, $30^{\circ}42^{I}$E) (Figure 2.2) lies on the eastern slopes of the Drakensberg Mountains within an elevation range of 1 500 - 1 800 m.

Geologically the area consists of three igneous rock formations with the overlying soil strata of the Timeball Quartz Series of the Transvaal System. These rock formations constitute bands of quartzite separated by shales and lavas, typical of the Pretoria Formation. Deeper soils are dystrophic latasols (Schackleton and Walker, 1985) of the Inanda Series (MacVicar, Loxton, Lambrechts, Le Roux, De Villiers, Verster, Merryweather, Van Rooyen and Von M. Harmse, 1977). These latasols are characterised by a humic A-horizon and a B-horizon of moderate (30 - 40%) clay content (Figure 2.3) (Schackleton and Walker, 1985). The nutrient status of the soil prior to amendment through the application of inorganic fertilizers is presented in Table 2.1. The soils are well drained and highly leached, and a comparison of Tables 2.1 and 2.2 shows the soils of MSNR to be as nutrient poor as strongly leached heathland soils [with the possible exception of total N which, at 0.14% is marginally higher than the 0.12% proposed by Day (1983) as the upper limit of nutrient-poor heathland soils].

The climate at MSNR can be described as moderate to cool with frequent mists (approximately 100 days per annum). The mean annual rainfall for the six year study period was 996 mm, 49% of which falls during the summer months of December, January and February. Mean annual minimum and maximum temperatures, measured at a height of 2 m were 10.4° C and 21.0° C respectively, while mean relative humidity was 65.9% with a mean low and mean high of 34.6 and 88.5% respectively. Ground frosts are common between April and

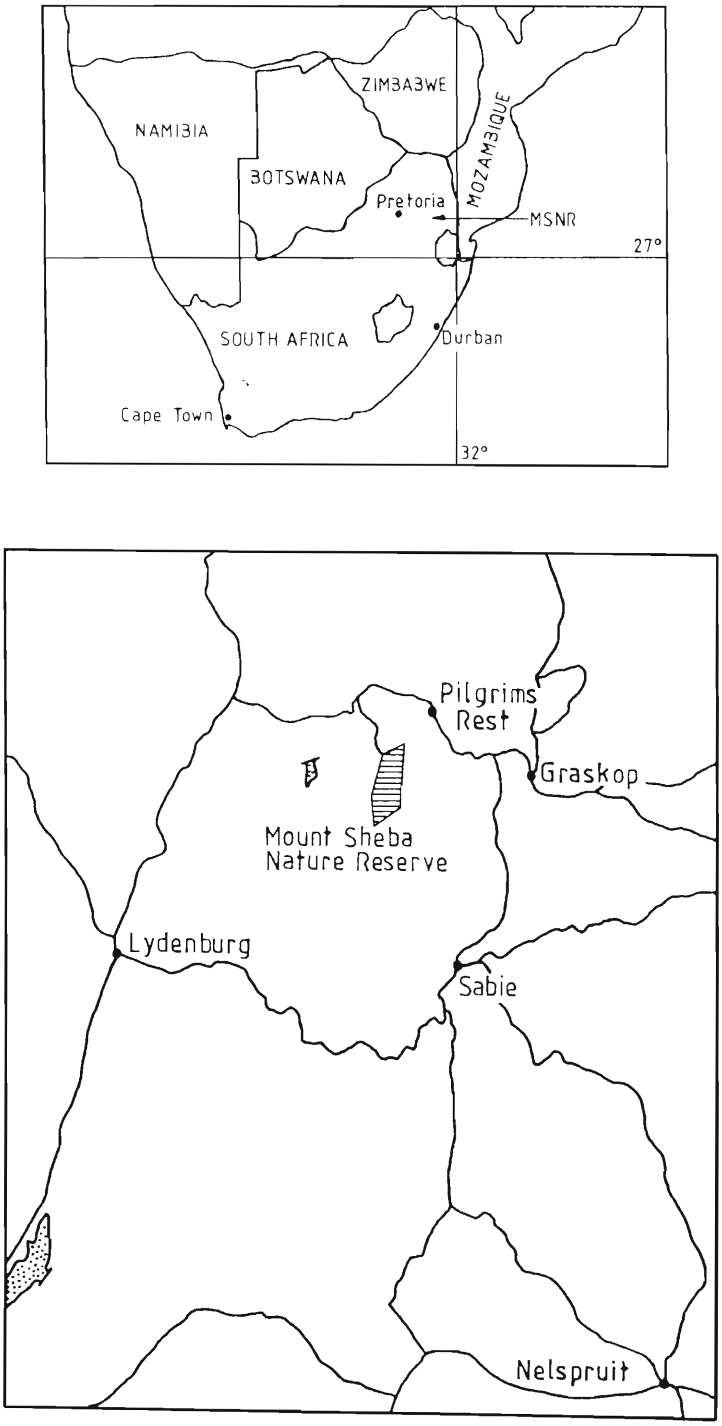


Figure 2.2 Map showing the locality of the study site, Mount Sheba Nature Reserve.

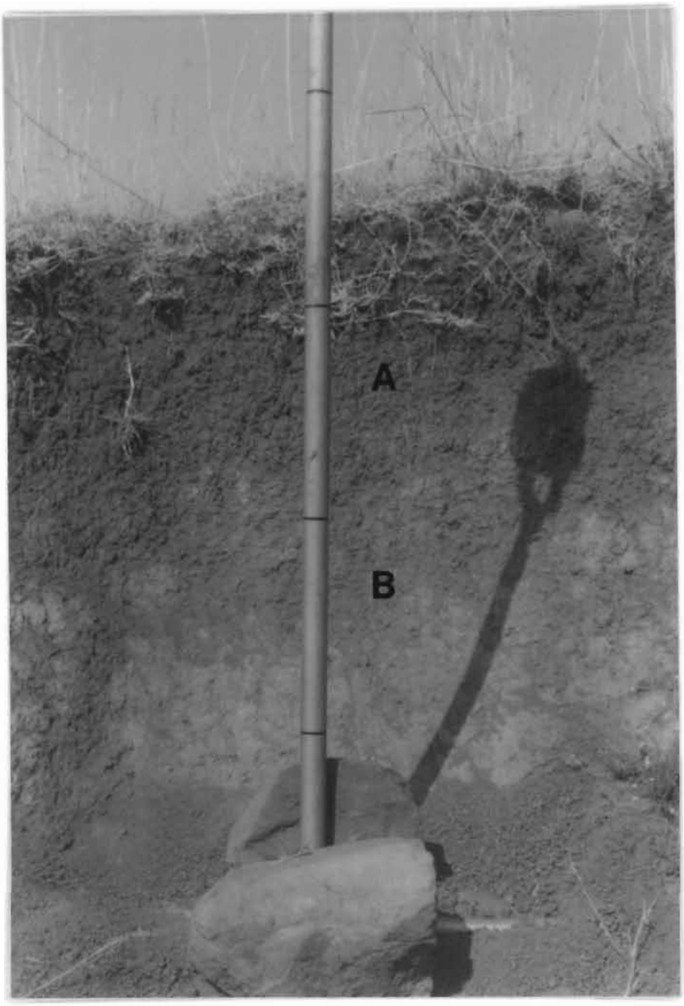


Figure 2.3 Soil profile of Inanda Series Soil on which *P. neriifolia* shrubs were cultivated. Note the [A] and [B] horizons.

Table 2.1 Mineral concentration of the soils of the Mount Sheba Nature Reserve protea cultivation site prior to the addition of inorganic fertilizers. Values are the means (± one standard deviation) of 105 replicates taken over 2.5 years. For comparative purposes with data from other regions, the mean concentration of certain nutrients is shown in mg kg^{-1}.

Mineral	**mmol kg^{-1}**	**mg kg^{-1}**
Sodium	0.44 ± 0.27	10.16
Potassium - total	8.80 ± 1.38	343.20
Potassium - avail	1.19 ± 0.35	46.53
Calcium	1.60 ± 0.87	64.13
Magnesium	1.07 ± 0.40	26.01
Phosphorus - total	2.26 ± 0.63	70.06
Phosphorus - avail	0.35 ± 0.11	10.84
Nitrogen - total[a]	100 ± 21.43	1400.00
Nitrogen - soluble	1.68 ± 0.47	23.53
pH (water)	4.85 ± 0.24	
CEC [b]	0.69 ± 0.29	
Texture [c]	sand 40 : clay 34 : silt 26	

[a] equals 0.14%.

[b] cation exchange capacity (me 100 g $^{-1}$).

[c] (%).

Table 2.2 Soil nutrient levels characteristic of different soil types in mediterranean ecosystems.

	Nutrient-poor Strongly-leached	**Nutrient-rich Moderately-leached**	**Agriculturally-rich Weakly-leached**
Total N (%)	<0.12[a] 0.04 - 0.10[b] 0.046[c]	0.12 - 0.30[a] 0.04 - 0.50[b] 0.443[c]	> 0.30[a]
Total P (%)	< 0.022[a] 0.0015 - 0.0027[b] 0.00015[c]	0.022 - 0.06[a] 0.015 - 0.0075[b] 0.0026[c]	> 0.06[a]
Total exchangable cations (me 100 g^{-1})	5.0[a] 4.3[b]	10.0[a] 3.22[b]	23 - 44[a]
pH	3.5 - 5.0[b] 4.2[c]	4 - 7[b] 5.1[c]	

[a] Day (1983)

[b] Specht and Moll (1983)

[c] Pierce and Cowling (1983a,b)

July and light snow was recorded once in July 1987. Two severe hailstorms occurred - in December 1986 and June 1989. The effects of hail on results presented in this thesis will be noted where applicable.

Monthly rainfall and temperature data for the periods 1984 - 1987 (before fertilizer additions) and 1987 - 1989 (after fertilizer additions) are shown in Figures 2.4 and 2.5 respectively.

2.1.3 **Cultivation practices**

Proteas are cultivated on the mountain slopes in contoured rows which are 1 m wide and 5 m apart (Figure 2.6). The rows run at a 2^0 gradient along the slopes and are cultivated to a depth of 0.5 m. Planting of nursery-grown seedlings, to a depth of 0.3 m and 1 m apart, is done in November after the spring rains. Planting density is 1 000 shrubs per hectare. New plantings are left for three months after which a 1 m wide, 50 μm thick strip of black plastic mulch (Gunmulch) is laid along the line, slit longitudinally, and placed on the ground around the young shrubs. The plastic is covered with approximately 25 mm loose soil and rocks to prevent deterioration by sunlight. Mulching serves to reduce soil moisture loss during the drier winter months and it also reduces weed competition. There is no irrigation.

Plantation maintenance includes the daily harvest of all flowers, mowing of grass between lines, removal of dead branches, pruning and mechanical weed control. Orchards are sprayed (200 ℓ ha^{-1}) monthly with fungicide (for example, Benlate at 1g ℓ^{-1}) and every three months with insecticide (for example, the synthetic pyrethroid Decis at 0,5 ml ℓ^{-1}) to reduce pest and pathogen incidence. During the study period experimental shrubs were treated in the same way as other shrubs in the orchards except that there was no pruning. Where branches did die

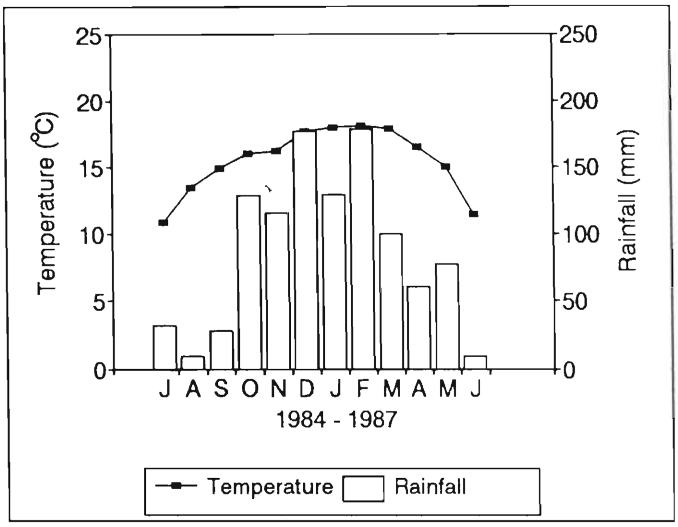


Figure 2.4 Mean monthly temperature and mean monthly rainfall for the period 1984 - 1987 at Mount Sheba Nature Reserve.

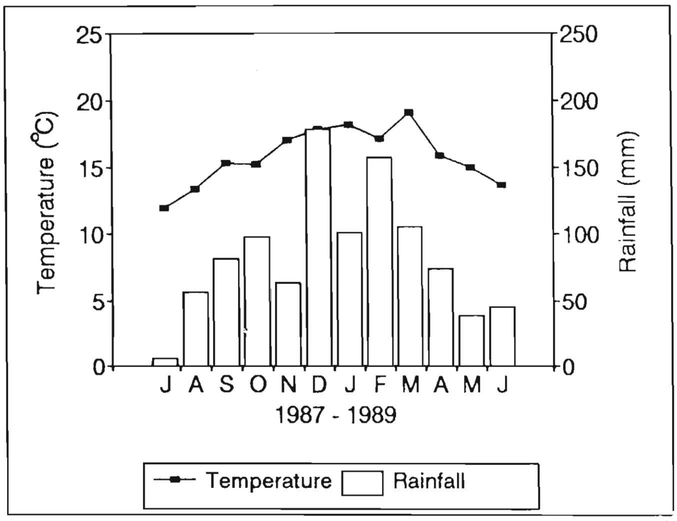


Figure 2.5 Mean monthly temperature and mean monthly rainfall for the period 1987 - 1989 at Mount Sheba Nature Reserve.

Figure 2.6 General view of protea orchard at Mount Sheba Nature Reserve. Proteas are planted in lines that are contoured to a 2° slope. Lines are 5m apart and plant spacing in the line is 1m. Planting density is 1 000 shrubs per hectare.

and break off the shrubs, this was recorded as part of the shrub litter.

The shrubs designated for this study were 100 shrubs in two lines on a slope. Replicates for the various measurements and studies contained within this thesis were selected from these 100 shrubs.

2.1.4 Duration of study and the timing of measurements

The *P. neriifolia* cv. Kouga shrubs studied in this investigation were grown from seed germinated in June 1979 and planted into the orchards in November 1980. Investigations commenced in April 1984 when shrubs were approximately five years old, and continued until February 1989 when shrubs were approximately 10 years old. Investigations were terminated a year earlier than planned due to damage and death of the shrubs (Figure 2.7) as a result of a severe hail storm in June 1989.

Initially, all measurements were conducted either monthly, bimonthly or every three months. This was possible while the researcher was resident at the cultivation site. However, from January 1988 to June 1989 the researcher was not resident and measurements were made at longer intervals but at least every three months.

Inorganic fertilizers were applied for the first time in April 1987. Thereafter they were applied at approximately three monthly intervals through to the end of the study.

Figure 2.7 View of *P. neriifolia* study shrubs following a severe hail storm in June 1989.

2.2 Growth measurements

2.2.1 Shrub architecture

2.2.1.1 Whole shrub dimensions

A number of whole shrub dimensions were measured on an annual basis. Shrub height was measured from the base of the main stem to the tip of the highest growing shoot. A pair of calipers was used to measure the diameter of the main stem at a height of 300 mm above the soil level. Cross-sectional shrub dimensions were measured in two directions: along the row and across the row in which the shrubs were cultivated. These measurements reflect the furthest extension of shrub growth in each of the two directions.

From these measurements additional shrub dimensions were calculated. Canopy radius was calculated as half the mean of the two cross-sectional shrub dimensions ie. along and across the row. Projected canopy area was calculated as for the area of a circle using the average canopy radius, and shrub volume was calculated by multiplying canopy area by shrub height (Van der Pas, 1972). It is important to note that there is no bare stem since leaves do occur close to ground level. Therefore, the bottom of the canopy is equivalent to ground level.

In April 1986, the above-mentioned dimensions were recorded for ten shrubs after which they were removed from the field and returned to the laboratory. In the laboratory the shrubs were separated into components viz. leaves, stems, flowers and buds, non-proteoid and proteoid roots. Fresh mass was recorded for each component and thereafter, sub-samples of components were oven dried (80° C) to a constant mass. Using sub-sample moisture contents, component and whole shrub dry mass were calculated.

Using the dimensions obtained for the ten shrubs above a number of possible allometric relationships were investigated between shrub dimensions and shrub dry mass or component dry mass. The most reliable correlation was found between the diameter of the main stem and whole shrub dry mass ($r=0.67$; $n=10$), and this was used in 1987 for the estimation of whole shrub dry mass. The calculation used was as follows:

shrub dry mass = (0.059 x stem diameter) - 0.41 . . . (a)

In February 1989 a similar study was carried out in which three replicates each from the three field fertilizer trial sites were removed for whole shrub and component analysis. Methods were the same as for the 1986 investigation and the absolute values obtained were used to describe whole shrub and component dry masses four months prior to the death of the shrubs. Combining the three shrubs from each of the three fertilizer treatments, the allometric relationship calculated in February 1989 ($r=0.74$; $n=9$) compared favourably with that calculated in April 1986 ($r=0.67$; $n=10$). Shrub dry mass for 1988 was estimated using the 1989 allometric relationship shown below:

shrub dry mass = (0.252 x stem diameter) - 9.13 . . . (b)

Using shrub component dry masses for 1986 ($n=10$) and 1989 ($n=3$ per fertilizer site), it was possible to calculate a leaf/stem dry mass ratio and a shoot/root dry mass ratio.

2.2.1.2 **Leaf area determinations**

During 1986 and 1987 (April to April) and 1987 to 1989 (June to February) the leaf area of leaves on newly produced shoots was measured. Initially, the outlines of 120 leaves were traced on to paper. These leaf shapes were cut out and the paper leaves weighed. Leaf area was determined by comparing the paper leaf masses to the mass of a known area of the same paper. Leaf length was also measured and a correlation between leaf length and leaf area obtained ($r=0,975$; $n=120$). All future leaf areas were determined by measuring leaf length and applying the allometric relationship using the calculation below:

$$\text{leaf area} = (0.095 \times \text{leaf length}) - 0.89.$$

During 1986/1987, the leaf area of 25 replicate shoots was measured at each interval (approximately every two months) and during 1987/1989, leaf areas were determined on five replicates each per fertilizer treatment (approximately every three months). This allowed for the investigation of possible seasonal variations in leaf area. For each sample period, for each shoot, shoot length and diameter were also measured allowing for the expression of leaf area as leaf area per stem cross-sectional area (mm^2 mm^{-2}). The dry mass of leaves was also determined by oven drying the leaves at 80° C to a constant mass.

From leaf area determinations it was possible to calculate the leaf area ratio (F) of the shrubs. Leaf area ratio is a measure of the 'leafiness' of the plant and can be calculated as:

$$F = \frac{\text{leaf area}}{\text{plant dry mass}}$$

(Hunt, 1978; 1982)

Furthermore, leaf area index (L), which relates the ‘leafiness’ of the shrub to the ground area covered by the shrub canopy (Hunt, 1982), could be calculated. Shrub canopy areas previously calculated (Section 2.2.1.1) were projected to ground area for the calculation of leaf area index:

$$F = \frac{\text{total leaf area of shrub}}{\text{ground area covered by shrub}}$$

(Hunt, 1978; 1982)

Leaf area index was calculated in April 1986 and February 1989 only. For these two periods actual shrub dry mass and component dry mass were determined on 10 and 3 x 3 replicates, respectively, as described earlier. Knowing the mass of leaves and the specific leaf area (Section 2.2.1.3), it was possible to calculate total leaf area of the shrub. However, it is important to note that the leaf area index calculated in this study was specific for the *P. neriifolia* shrubs and does not refer to a community leaf area index.

2.2.1.3 Leaf longevity and leaf nutrient concentration

In July 1986, 100 newly produced leaves were tagged (five leaves on each of 20 shrubs). Initially monthly, and after January 1988 three-monthly, tagged leaves were recorded as either being present or absent. Where possible, an attempt was made to confirm absent leaves as having fallen from the shrub by collecting the leaves from the litter layer. The study ran for a period of 32 months and from this data an estimation of leaf longevity was possible.

In conjunction with leaf longevity measurements, changes in levels of leaf N, P and K with age were determined over a period of 32 months. In July 1986, 600 newly produced leaves were marked as having been produced within the previous month (200 leaves per future fertilizer site). Initially monthly, and later at three-monthly intervals, leaves (n=10 per sample period) were removed and N, P and K levels determined (Section 2.4.1). Prior to nutrient determinations, specific leaf area was calculated for individual leaves as follows:

$$\text{Specific leaf area} = \frac{\text{leaf area}}{\text{leaf dry mass}} \qquad \text{(Hunt, 1978; 1982)}$$

2.2.1.4 **Flower size**

Following the application of inorganic fertilizers to field cultivated shrubs (Section 2.6), flower head dry masses were monitored from June 1987 to June 1989. For each sample period and for each fertilizer site the number of replicates varied depending on the number of flowers present. A minimum replication of ten was attempted but not always possible. Flowers were harvested and flower heads (florets and bracts only) removed. Flower heads were oven dried at 80° C to a constant mass and dry mass recorded.

2.2.2 ***P. neriifolia* phenology**

Phenological measurements were made for the periods: July 1984 - June 1985, July 1985 - June 1986, July 1986 - June 1987, and July 1987 - February 1989. Measurements were taken to record the growth, timing and periodicity of the following: shoot growth, flower production, and proteoid and non-proteoid root growth.

2.2.2.1 **Shoot growth**

For the periods 1984/1985, 1985/1986 and 1986/1987 the phenology of ten *P. neriifolia* plants was studied. On each shrub, ten apical shoots (termed primary shoots in this study) were tagged at the most recent transition area between the previous and latest growth flush. Tagging was done in July when new growth is usually initiated. Each month, shoot lengths (from tag to apex) were measured. Lateral shoots, produced from primary shoots, were tagged on bud sprouting and the same measurements performed. Also, a monthly record of the vegetative/floral status of the shoots was kept. When flowers were regarded as sufficiently developed for commercial harvest they were cut. Lateral shoots produced subsequent to flower harvest were tagged and measured as above. Monthly growth increments were calculated by subtracting the shoot length at the previous measurement date from the current shoot length. For simplicity, the growth and phenology of primary and secondary shoots are handled separately.

For the period 1987/1989 shoot growth measurements were made in a similar way as described above. However, there were a number of important differences in method. In this study ten apical shoots on five shrubs per each of the three fertilizer sites were tagged and measured. Measurements were made monthly until January 1988, thereafter approximately every three months. Unlike the previous study, in this study flowers were not removed. Rather the continuous production of lateral shoots and secondary lateral shoots (ie. lateral shoots from lateral shoots) was monitored. Growth increments were calculated as above and data groupings as detailed above were maintained.

2.2.2.2 **Flower production**

Of the 100 study shrubs, ten were used for litter production and ten for shoot growth measurements. Flower production was monitored at weekly intervals on a continuous basis from April 1984 to June 1989 on the remaining 80 shrubs. In the case of shrubs used for litter production and shoot growth measurements, flowers produced were counted and marked with paint. Where shrubs were removed for whole shrub mass determinations (Section 2.2.1.1), amendments to replicate number were made.

Flowers were removed when they were regarded as being sufficiently developed for commercial harvest. A record of the number of flowers produced per bush was kept from the inception of the study (including bushes where flowers were counted and marked with paint). This facilitated a study of flower production with increasing shrub age as well as a comparison of flower production with and without the addition of inorganic fertilizers. Flowers were returned to the laboratory where samples of standardised flowers with a stem length of 200 mm were oven dried at 80° C to a constant mass. Total dry mass removed was then calculated.

2.2.2.3 **Proteoid and non-proteoid root growth**

P. neriifolia shrubs used in the investigation of proteoid and non-proteoid root growth were not from the original 100 shrubs designated for the entire study. This is due to proteoid roots being very sensitive to disturbance which can be lethal to the plants (Vogts, 1982; Lamont, 1986). As the method for monitoring root growth involved soil/root cores, plant death may have resulted. Hence, ten shrubs not being studied in any other respect were used. These shrubs were immediately adjacent to the 100 study plants and it is interesting to note that shrub death did not occur.

Soil cores (three per shrub) were taken from a circumference line 300 mm from the main stem of the shrub. The black plastic mulch was removed and soil cores taken using a standard soil auger. After the cores were taken, the plastic mulch was replaced. Cores represented a depth range of 0 - 200 mm and the volume of each core was 1110 cm^3. The samples were sieved through a 2 mm mesh and roots separated into proteoid and non-proteoid components. As there was some difficulty in separating proteoid roots from the small non-proteoid rootlets, all rootlets with a diameter $\leq$ 1 mm were considered part of the proteoid root component. Both root types were oven dried at 80° C to a constant mass and dry mass recorded. Proteoid and non-proteoid root occurrence was expressed as g root material per 100 g soil dry mass.

Since proteoid root occurrence may be related to soil moisture levels (previously cited), the fresh and dry mass of the soil from the various samples was determined. Soil moisture content was expressed as a percentage of the dry mass of the soil.

The occurrence of both root types was monitored for one season only, from July 1986 to June 1987.

2.2.3 Litter production and decomposition

2.2.3.1 Litter production

Litter traps large enough to collect the entire litter fall from a shrub were erected beneath ten *P. neriifolia* shrubs. Litter collection continued for the entire duration of the study. Initially traps were cleared of all litter every two months and latterly in the investigation, approximately every three months. Collected litter was returned to the laboratory where it was sorted into leaf, stem and floral litter. Following the fresh mass measurement of the components, sub-samples were oven dried (80° C) to a constant mass allowing the calculation of total, leaf, stem and floral litter dry mass. Chemical analysis of litter was performed as described in Section 2.4.1.

Initial replication prior to the application of inorganic fertilizers was ten. This was reduced to three, three and four per fertilizer site after the application of inorganic fertilizers (indicated in the results where applicable).

2.2.3.2 Leaf litter decomposition

Leaf litter decomposition was measured in two separate trials.

In the first trial, every month, leaf litter of known fresh mass was placed into black litter bags (100 x 150 mm with a 2 mm mesh size) and three bags were placed beneath each of ten shrubs in the litter layer in the field. Bag sets (n=30) for each month were left in the field for three months after which litter bags were retrieved. In the laboratory leaf litter in the bags was reweighed. Mean monthly initial decomposition rates were calculated as follows: total decomposition over the three month period was apportioned equally to each month. As new litter bags were placed in the field every month, three decomposition values were obtained for each month. The mean of these was taken as the monthly decomposition rate.

In a second decomposition trial, 60 litter bags (100 x 150 mm with a 2 mm mesh size) with leaf litter of known fresh mass were placed beneath ten shrubs in the litter layer in the field. Initially at two monthly intervals and latterly at three monthly intervals ten bags were retrieved. In the laboratory leaf litter in the bags was reweighed and and leaf litter decomposition rate for the period calculated. Samples of the partially decomposed leaf litter were analysed for N, P and K (Section 2.4.1) to determine the release of these minerals into the soil. The trial ran for 487 days during which leaf litter decomposition and N, P and K release rates were monitored.

2.3 Nutrient status measurements

2.3.1 Shrub nutrient status

Shrub nutrient status was measured at three-monthly intervals prior to (n=10) and during the application of inorganic fertilizers (n=10 per fertilizer site). For each sample period the same shrubs were used for material collection although some rearrangement was required at the start of field fertilization.

For leaf and shoot nutrient analyses, newly produced vegetative shoots were selected. The youngest leaves and the segment of shoot supporting these leaves were collected and analysed for N, P and K (Section 2.4.1). For flower nutrient status analyses, flowers regarded as sufficiently developed for commercial harvest were analysed.

Florets and bracts were analysed separately for N, P and K using the methods detailed in Section 2.4.1.

Root nutrient status was measured for both proteoid and non-proteoid roots in November 1988 and February 1989. Soil/root sample cores were collected by the same method described in Section 2.2.2.3 except in this instance cores were taken from the original 100 test shrubs (5 replicate shrubs per fertilizer site). Once roots were separated into proteoid and non-proteoid components they were thoroughly washed in distilled water to remove all adhering soil. Thereafter, root samples were oven dried (80° C) to a constant mass and analysed for N, P and K (Section 2.4.1). This study was prematurely terminated by the death of the shrubs due to a hailstorm described in Section 2.1.4. As a consequence, seasonality in root nutrient status could not be monitored.

2.3.2 Soil nutrient status

Soil nutrient status was monitored for the entire duration of the investigation.

Prior to and during fertilization, soil samples (200 mm depth) were taken every three months. For each sample period prior to fertilization three replicates from five sample sites within the line in which the shrubs were growing were collected. Each replicate consisted of four randomly selected soil cores. For each sample period during fertilization three replicates from three sample sites for each fertilizer site were collected. Again, each replicate consisted of four randomly selected soil cores. In each case, samples were mixed, coned and quartered and analysed within 36 h.

Chemical analyses were performed initially by a private laboratory (April 1984 - December 1987) and latterly by the South African Sugar

Association (SASA) Experiment Station soil laboratories (January 1988 - February 1989). This is excepting nitrogen determinations which were all performed by the private laboratory. The laboratories used different soil analysis techniques, details of which are presented in Section 2.4.2.

As a result of the laboratories using different soil analysis techniques there was considerable variation in certain soil mineral levels. Therefore, data on seasonal variations in soil nutrient availability are presented for N, P and K only. For the remainder of the soil nutrients measured, data collected over the pre-fertilization study period were bulked and a mean value for the entire period is presented to indicate soil nutrient status. Similarly, for the three fertilizer sites, data for each site were bulked and a mean for the entire study period is presented.

2.4 Chemical analysis methods

2.4.1 Plant material analysis

Plant material chemical analyses were carried out by the author and the South African Sugar Association chemistry laboratories. Techniques used were the same and are standard techniques for the analysis of plant material by SASA. For all plant material samples only N, P and K determinations were carried out.

Samples of plant material (0.25 g) were added to a 100 ml long-necked Kjeldahl flask to which 2 ml of selenised concentrated sulphuric acid was added. The digestion was carried out for 1.5 h after which the digestion solution was made up to 25 ml with distilled water.

N was determined by Kjeldahl distillation. The digests were distilled with 12 ml 40% w/v sodium hydroxide and the ammonia given off was collected in a boric acid indicator solution. 0.01 M hydrochloric acid was then titrated against this solution and the volume of HCl recorded. The concentration of nitrogen in the plant tissue was then calculated.

P determinations were made using the molybdenum blue colorimetric assay. Ammonium molybdate (0.5 ml) (0.025 g ml^{-1}) and 0.5 ml stannous chloride reductant (0.002 g ml^{-1}) were added to 2 ml aliquots of the diluted digests. The reagents were thoroughly mixed and stood for 30 min to allow for colour development. Absorbances were read on a spectrophotometer at a wavelength of 700 nm. Plant material P levels were determined using standards.

Plant material K levels were determined using an atomic absorption spectrophotometer. Absorbances of digest aliquots were read at a wavelength of 766.5 nm and K levels determined from standard curves.

2.4.2 Soil analysis

2.4.2.1 Private laboratory

The private laboratory which carried out certain soil analyses was Labserve Analytical Services, P.O. Box 1920, Nelspruit, 1200, South Africa, and details of the methods described were supplied by Mr. K. Auerswald.

Soil pH was measured electrometrically. Fresh soil (40 g) in a 150 ml beaker was covered with 100 ml distilled water and gently shaken for 5 min. The mixture was then stood for 15 min after which the pH of the supernatant was measured.

Available soil Na, K, Ca, Mg and P were determined by a modified ISFEI (International Soil Fertility Evaluation and

Improvement Project) (Hunter, 1974) extraction procedure, AMBIC-1 (ammonium bicarbonate - 1). The extracting solution consisted of 197.6 g ammonium bicarbonate, 29.3 g ethylenediamine tetra acetic acid and 3.7 g ammonium fluoride. Reagents were mixed with 20 l distilled water and allowed to stand overnight after which the pH was adjusted to 8.1 with ammonia or acetic acid.

Soil samples were thoroughly mixed and sieved through a 1 mm mesh sieve. 5 g of sample was placed into a plastic bottle to which 50 ml AMBIC-1 extractant was added. The soil and extractant were then swirled and allowed to stand for 20 minutes. The bottle was then tightly capped and shaken in a mechanical shaker at 180 oscillations min^{-1} for exactly 30 min (timing was critical as further shaking could result in more elements being extracted). After shaking two drops of flocculent were added and bottles swirled to mix. All sample aliquots were taken from the supernatant liquid.

For Na and K determinations 8 ml supernatant aliquots were read directly on an atomic absorption spectrophotometer (AA) (589 and 766.5 nm respectively) using an acetylene flame and an angled burner (75° and 180°, respectively). The AMBIC-1 extraction solution was used to zero the AA and soil mineral levels were calculated using Na and K standards.

For Ca and Mg determinations, 2 ml supernatant was mixed with 1 ml acetic/hydrochloric acid (1:1) mixture. After foaming had ceased 2 x 3.5 ml of a mixture of 100 ml 10% lanthanum chloride and 4 ml distilled water were added and well mixed and any precipitate allowed to settle. Ca and Mg were then read on the AA (422.7 and 285.2 nm respectively) with an acetylene flame and an angled burner (30° and 90°, respectively). The AA was zeroed on distilled water and levels of minerals calculated using standard solutions.

For phosphorus determinations the antimony potassium tartrate - ascorbic acid method was used. Antimony potassium tartrate (4 g) was dissolved in 400 ml distilled water. Concentrated sulphuric acid (500 ml) was added to this and allowed to cool. Once cool this solution was added to a second solution of 30 g ammonium molybdate dissolved in 300 ml distilled water. The resultant solution was made up to 1 l with distilled water and stored in the dark in a refrigerator. Ascorbic acid (4 g) was dissolved in 100 ml distilled water and added to 3 g gelatine dissolved in 400 ml warm water. Ammonium molybdate solution (200 ml) was then added to the gelatine ascorbic acid solution and the new solution made up to 1 l with distilled water. AMBIC-1 extract supernatant (4 ml) was pipetted into a plastic bottle. If the extract was coloured, 1 ml of concentrated sulphuric acid was added. Distilled water (85 ml) and 10 ml of the ammonium molybdate ascorbic acid gelatine solution were added to the extract. The contents were stirred and left for 30 min to allow for colour development. P levels were then read on a spectrophotometer at a wavelength of 743 nm using a chromium lamp. The machine was zeroed using the AMBIC-1 extracting solution and P levels were calculated using standard solutions.

Soluble N was determined by extracting in 1 M potassium sulphate. The solution was then digested by the Kjeldahl digestion procedure viz. 3 ml concentrated sulphuric acid, half a selenium and half a copper catalyst tablet. The digests were then mixed with sodium salicytate, sodium nitroprusside and dichloro-isocyanuric acid and N levels read on a spectrophotometer at 660 nm. Total N was measured in the same way except samples were not extracted in potassium sulphate. Rather, soils were digested directly. Thereafter colour development and absorbance measurements were the same as above.

Total levels of N, P and K were measured at the start and end of the study. Samples (1g) were digested in a mixed acid digest consisting of 1ml concentrated perchloric acid, 5ml concentrated nitric acid, and 0,5ml concentrated sulphuric acid. Nutrient levels were determined using the respective procedures outlined above.

Soil field capacity measurements were determined on 36 samples. Samples were saturated with water and then drained to equilibrium at a pressure differential of 33 kPa. Samples were weighed and then oven dried (80° C) to a constant mass. Field capacity was expressed as a percentage of the dry mass of the soil.

2.4.2.2 SASA laboratory

Mr. J. Meyer, Head of Chemistry, SASA Experiment Station, P.O. Box X02, Mount Edgecombe, 4300, South Africa, provided details of the soil analysis methods used by the SASA laboratories. For ease of comparison to the soil analysis methods used by the private laboratory, methods used by the SASA laboratory are described briefly, principally to highlight differences in methodology.

Prior to the extraction of soil samples, soils were oven-dried (45° C) overnight. Soil pH was determined by the same method as used by the private laboratory. For soil available cation (Na, K, Ca and Mg) determinations, a 10 g soil sample sieved through a 2 mm mesh was extracted in 100 ml 1 N ammonium acetate. The sample was shaken at ambient temperature for 20 min using a reciprocal shaker. After centrifugation of the sample, supernatant aliquots were removed for mineral determinations on a Varian 10/20 atomic absorption spectrophotometer (AA). Details of the AA settings for each of the cations are presented in Table 2.3. Available phosphorus was determined by the Truog method where 2 g of finely ground soil sample was extracted in 100 ml 0.02 N sulphuric acid. The sample was shaken at ambient temperature for 20 minutes using a reciprocal shaker. After centrifugation of the sample a supernatant aliquot was removed for P determination on a spectrophotometer at 695 nm. The reagent used for colour development was ammonium molybdate ascorbic acid, as described in Section 2.4.2.1.

2.4.3 **Rainwater collection and analysis**

Rainwater samples were collected on a continuous basis for the period July 1986 to June 1987 according to the method described by Likens, Bormann, Pierce, Eaton and Johnson (1977). Samples (20 ml) were preserved in 2 ml concentrated sulphuric acid and 5 ml chloroform (Allen, Grimshaw and Holdgate, 1974). When samples were sent to the SASA laboratory for chemical analysis the chloroform interfered with mineral determinations, particularly using the atomic absorption spectrophotometer. Attempts at evaporating the chloroform under vacuum failed and samples had to be discarded.

A second rainwater collection was initiated in November 1988 but by this time the researcher was no longer resident at the study site. Therefore, rainwater could be collected only at specific times when the researcher was present for field measurements. Rainwater, shrub leaching and throughfall, and shrub stemflow were measured during November 1988 and February 1989.

Rainwater (n=5) was collected according to the method described by Likens *et al.* (1977). Shrub leaching and throughfall was measured by placing collecting containers (n=5 per shrub) of known area beneath three shrubs per fertilizer site. Stemflow was measured by firmly tying aluminium foil collecting vessels on the main stem of the shrubs (n=3 shrubs per fertilizer site) below the first branching. The volume of water collected in each instance was recorded and converted to an area basis depending upon the sizes of the shrubs. Water samples collected in each instance was retained for chemical analysis. The researcher did not have the facilities to measure runoff or streamflow. These data were obtained from agricultural consulting engineers (Personal communication, K. van Rensburg, Murray, Biesenbach and Badenhorst, P.O. Box 498, Nelspruit, 1200, South Africa). Streamflow, which is a combination of runoff and leaching, was calculated using rainfall, aspect and soil data supplied by the researcher. Streamflow, inclusive of runoff, seepage and percolation to the impermeable rock layer at 2 m, was calculated to be an average 31.8% of total rainfall. However, it must be noted that the catchment feeding the stream for which streamflow was calculated did not consist only of protea orchards. Rather, protea orchards formed a small fraction (10%) of the catchment. However, in the absence of more specific data, these data, in conjunction with stream water samples (n=5) collected by the researcher for chemical analysis, were used in nutrient budget calculations.

All water samples were stored in glass bottles at 4° C and chemical analyses for N, P and K were performed within one week of collection.

All water samples were chemically analysed by the SASA laboratory using the same procedures and reagents as used for plant material chemical analysis (Section 2.4.1).

2.5 Seedling growth response to various combinations of N, P and K

The growth response of *P. neriifolia* cv. Kouga to various combinations of N, P and K was monitored in seedlings grown under nursery conditions. Using a 4 x 4 x 4 randomised block design, four levels each of N, P and K were tested. The concentration of the nutrients tested (Table 2.4) was based on previous nutrition studies on the Proteaceae by Nichols and Beardsell (1981), Thomas (1981) and Heinsohn (1983). Since nitrate nitrogen has been shown to be detrimental to protea growth (Claassens, 1981; 1986; Heinsohn, 1983), all N in this investigation was supplied in the ammonia form. Nutrients were supplemented with all other essential elements at half-strength Hoaglands nutrient solution (Sutcliffe and Baker, 1974). There were nine replicates for each treatment and ten control plants which received water only.

Seeds were germinated immediately prior to the experiment and once four leaves had developed seedlings were transplanted into standard nursery bags (250 x 150 mm) containing a 1:1 mixture of washed sand and vermiculite. Pots were kept in the open nursery and were watered daily with a mist spray. For one year seedlings were supplied their respective nutrient solutions as weekly 60 ml aliquots.

At the end of the study period seedlings were harvested and the roots and shoots were handled separately. Dry mass was determined by drying at 80° C to a constant mass. Shoot material was retained for the analysis of N, P and K as described in Section 2.4.1.

Table 2.3 Varian 10/20 atomic absorption parameters for soil cation determinations by SASA laboratory

Mineral	Burner Angle (°)	Flame	Wave-length (mm)	Slit (mm)
Na	75	Oxidising	489.0	0.5
K	180	Oxidising	766.5	1.0
Ca	30	Reducing	422.7	0.5
Mg	90	Oxidising	285.2	0.5

Table 2.4 Levels of N, P and K applied to seedlings of *P. neriifolia* grown in the nursery. There were four levels of each nutrient and all 64 possible combinations of N, P and K were tested. (Note: concentrations refer to the element).

Mineral	Concentration (mM)			
Nitrogen	1	4	7	10
Phosphorus	0.05	0.25	0.45	0.65
Potassium	0.05	0.45	0.85	1.25

Table 2.5 The chemical composition of Plantosan - the slow release fertilizer used in the fertilization of mature *P. neriifolia* shrubs.

Nutrient		**Concentration**
Macronutrients		
Nitrogen	mol kg^{-1}	14.28
Phosphorus	mol kg^{-1}	1.42
Potassium	mol kg^{-1}	3.20
Sulphur	mol kg^{-1}	0.94
Magnesium	mol kg^{-1}	0.99
Micronutrients		
Boron	mmol kg^{-1}	32.37
Copper	mmol kg^{-1}	9.44
Iron*	mmol kg^{-1}	17.91
Manganese	mmol kg^{-1}	9.10
Molybdenum	mmol kg^{-1}	5.21
Zinc	mmol kg^{-1}	3.82

* chelated with EDTA.

Plantosan is a Group 1 Fertilizer manufactured by FBC Holdings (Pty) Limited, P.O. Box 215, Chloorkop, 1624, South Africa.

Table 2.6 Annual delivery of N, P and K for each fertilizer treatment (assumes *P. neriifolia* roots occupied 4 m^2 ground area).

Fertilizer treatment	**Delivery level ($mol\ m^{-2}\ yr^{-1}$)**		
	N	**P**	**K**
Plantosan plus ammonium sulphate	3.340	0.212	0.480
Plantosan plus urea	5.970	0.212	0.480
Control	0	0	0

Dry mass and chemical data were subjected to multifactor analysis of variance (Sokal and Rohlf, 1981) to determine single or interactive effects of N, P and K at the four levels of application on seedling growth and chemical composition.

2.6 Fertilization of mature *P. neriifolia* shrubs

The results obtained from the nursery experiment formed the basis for the selection of inorganic fertilizers for the fertilization of mature *P. neriifolia* shrubs.

A urea-based slow release fertilizer (Plantosan) was selected for testing under field conditions. Plantosan has an NPK ratio of 5:1:3 (mass basis), a mixture of micronutrients (Table 2.5) and a release period of three months. Since seedlings showed a marked growth response to N (Section 4.1), the N levels of Plantosan were supplemented with ammonium sulphate and urea.

There were three fertilizer treatments: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU) and an unfertilized control (C). Fertilizers were applied every three months - Plantosan at a rate of 150 g per running metre and ammonium sulphate and urea at 80 g per running metre. These rates were recommended by the manufacturers of Plantosan and match as closely as possible the rate of N, P and K delivery by the NPK treatment which resulted in the best growth of seedlings in the nursery experiment. The annual delivery of N, P and K for each fertilizer treatment is given in Table 2.6.

In order that fertilizers would penetrate through the plastic mulch into the root layer and in order not to disturb the sensitive proteoid roots (Lamont, 1986), a 200 mm deep furrow was dug immediately alongside the lines in which the proteas were growing and fertilizers were applied into this furrow. It was assumed that soil water would carry the nutrients into the root layer. After fertilizers had been spread in the furrow, the furrow was filled to prevent fertilizer movement within the furrow should heavy rain occur. Each time fertilizers were applied the furrow was re-opened.

In Section 2.1.3 it was mentioned that the study plants were in two rows on a slope separated by a 5 m inter-row. The lower row of 51 plants was divided into two groups and these shrubs received PAS (n=25) and PU (n=26). The upper row plants (n=49) acted as unfertilized control plants. There could, therefore, be no leaching of fertilizers from fertilized to unfertilized shrubs. Due to the layout of the orchard no randomised experimental design could be implemented. However, since the history of the shrubs had been recorded for three years it was felt that differences between shrubs could be tested between treatments against the historical background.

3 GROWTH, PHENOLOGY AND NUTRIENT CYCLING IN A CULTIVATED *PROTEA NERIIFOLIA* ORCHARD

3.1 Shrub growth and architecture

The dimensions of seven year old *P. neriifolia* shrubs cultivated in a summer rainfall area are shown in Table 3.1. The data show that a shrub with a mean canopy area of 3.5 m^2 and shrub volume of 7.0 m^3 has a mean dry mass of 3.8 kg. Within one year the mean dry mass of the shrubs increased by a factor of 1.7 to 6.5 kg, indicative of active growth. It should be noted that all dimensions except stem diameter are affected directly by the harvest of flowers. The dimension along the line is less than that across the line as a result of the method of planting. With only one metre between shrubs, shrubs tended to grow to the area of least competition ie. the inter-row.

Table 3.1 also shows one of the problems of working with wild as opposed to highly bred flora viz. the great variation in results sometimes obtained. Despite the use of 100 replicates, standard deviations presented indicate considerable variation for certain shrub dimensions, for example, dimension along the line.

Figure 3.1 illustrates the respective contributions of the shrub components to shrub dry mass and it is evident that stems contribute up to 66% of total shrub dry mass. Leaves, flowers and buds contribute 14% and roots 10%. It is clear, therefore, that increases in plant dry mass are primarily a result of above-ground vegetative growth ie. stem and leaf production.

Using data supplied in Figure 3.1, a shoot/root dry mass ratio of 8.79 kg kg^{-1} can be calculated ie. nearly nine times more shoot than root material is present. A leaf/stem dry mass ratio of 0.303 kg kg^{-1} indicates that shoot dry mass primarily consists of stem material suggesting that the bulk of resources is used for wood production.

Table 3.1 Shrub dimensions of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The dimension data were collected in April 1986 and are the mean ± one standard deviation (SD) for 100 shrubs. Shrub dry mass for 1986 is the mean of the actual dry mass of ten replicates, and shrub dry mass for 1987 was determined from an allometric relationship (a) between shrub stem diameter and shrub dry mass.

Dimension		**Mean ± SD**
Height	m	2.0 ± 0.3
Stem diameter	cm	7.2 ± 1.6
Dimension along line	m	1.8 ± 0.5
Dimension across line	m	2.4 ± 0.5
Canopy radius	m	1.1 ± 0.2
Canopy area	m^2	3.5 ± 0.6
Canopy volume	m^3	7.0 ± 2.1
Shrub dry mass - 1986	kg	3.8 ± 0.4
Shrub dry mass - 1987	kg	6.5 ± 0.7

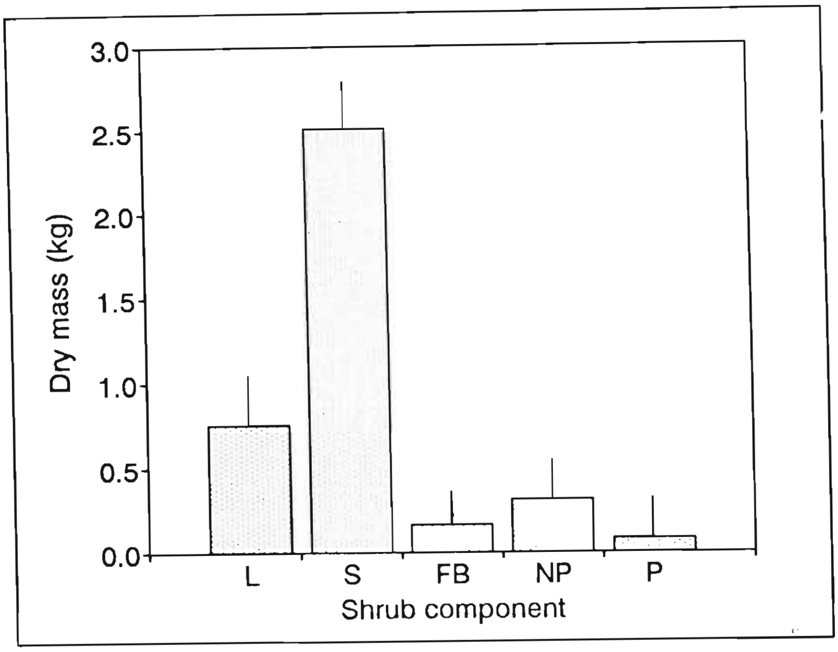


Figure 3.1 Dry mass of shrub components of seven year old *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. Values are the means (± one standard deviation) of ten shrubs dug up, separated into five components (leaves (L), stems (S), flowers and buds (FB), non-proteoid roots (NP) and proteoid roots (P)) dried and weighed.

As it was not possible to measure the total leaf area of the shrubs continuously, leaf area is expressed as leaf area per unit stem cross-sectional area. This is because leaf/stem ratios can vary due to stem and leaf growth, and stem cross-sectional area was thought to be the most constant. Cultivated *P. neriifolia* did exhibit seasonal variations in leaf area (Figure 3.2) with maximum leaf area per stem cross-sectional area being recorded in late spring (November). New shoots (stems and leaves) are usually initiated in June/July (winter) of any one year (Heinsohn and Pammenter, 1988). After shoot initiation, leaf area increases from July to November (winter to spring) probably as a result of leaf production and expansion. Leaf area remains relatively constant throughout the summer months until a reduction occurs in autumn (April). This reduction is probably a result of leaf loss which peaks in late winter (Figure 3.9) and also stem thickening with age.

Mean leaf area (LA), leaf area ratio (F) and leaf area index (L) for seven year old *P. neriifolia* cultivated in a summer rainfall area are presented in Table 3.2. The data are separated into three categories representing future fertilizer treatments although prior to fertilization each group of data per plant characteristic was strictly one sample. Analysis of variance and a multiple range test (MSD) showed that there were no significant differences among the group of plants chosen for future fertilizer applications ($P > 0.05$).

In comparison to other plants, seven year old *P. neriifolia* has a relatively low leaf area ratio and leaf area index. For example, the leaf area ratio of *Leucadendron salignum* seedlings was double that for mature, unfertilized *P. neriifolia* shrubs (Heinsohn, 1983), and the leaf area index of most evergreen trees of between 3 and 4 (Salisbury and Ross, 1978) is considerably larger than that recorded in Table 3.2 for *P. neriifolia*. The low leaf area ratio indicates that the shrubs do not have many leaves and the low leaf area index supports this finding in that it expresses a low leaf cover of the ground area above which the shrub canopy has grown.

Figure 3.3 illustrates the longevity of leaves of *P. neriifolia* cultivated in a summer rainfall area. Leaf longevity is presented as the number of leaves present as a percentage of the total number of leaves originally tagged. For the entire period

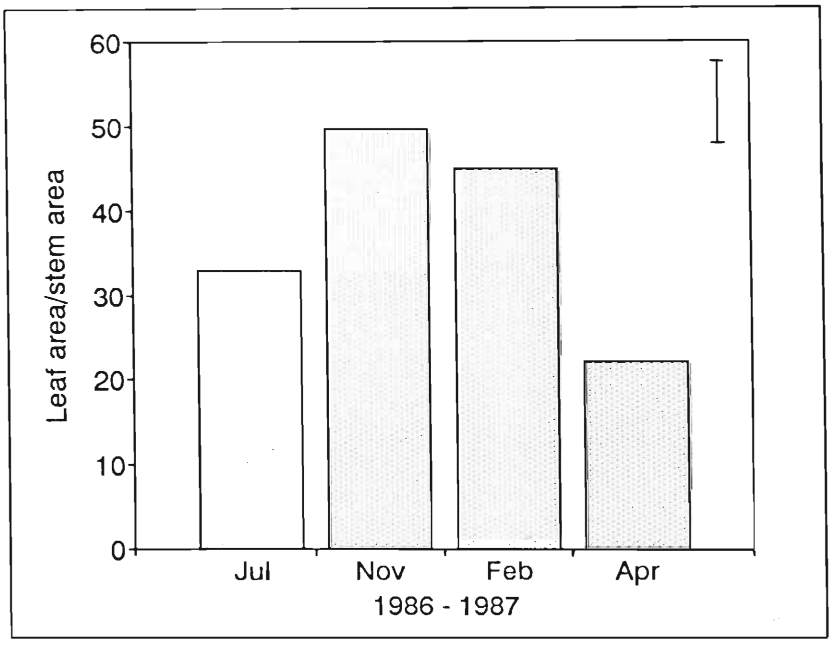


Figure 3.2 Seasonal variation in leaf area per stem cross-sectional area (mm^2 mm^{-2}) of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

Table 3.2 Mean leaf area per stem cross-sectional area, leaf area ratio and leaf area index for each future fertilizer treatment prior to the application of inorganic fertilizers to *P. neriifolia* cultivated in a summer rainfall area. The data are separated into three categories representing future fertilizer treatments although prior to fertilization each group of data per plant characteristic is strictly one sample.

Future fertilizer	**Leaf area/ stem area (mm^2 mm^{-2})**	**Leaf area ratio (m^2 kg^{-1})**	**Leaf area index (m^2 m^{-2})**
Plantosan plus ammonium sulphate	37.23	0.954	1.051
Plantosan plus urea	36.48	0.906	0.925
Control (no fertilizer)	37.81	1.002	1.052

Analysis of variance and a multiple range test (MSD) showed that there were no differences among the groups of plants chosen for future fertilizer applications ($P > 0.05$).

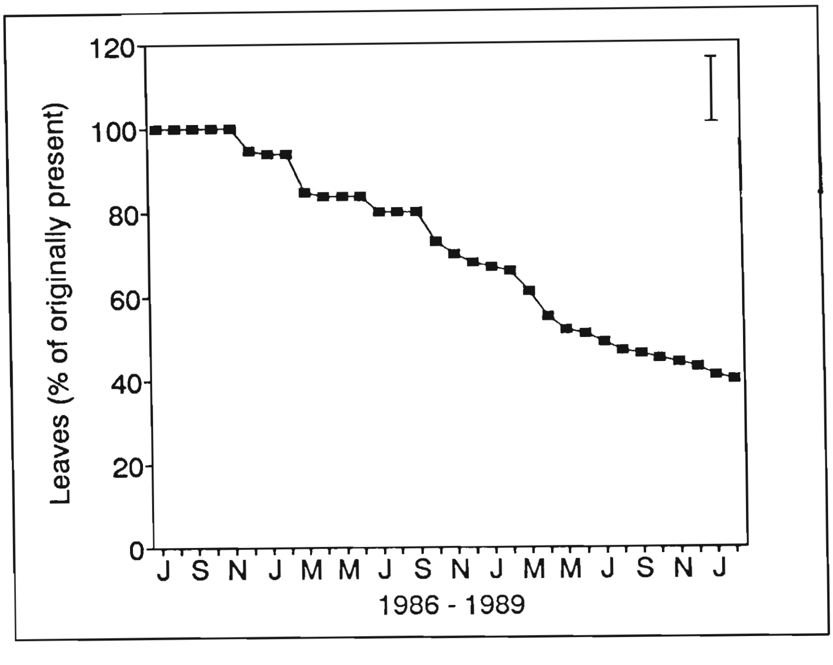


Figure 3.3 Leaf longevity, measured as a percentage of the total leaves tagged, of *P. neriifolia* cultivated in a summer rainfall area without the addition of inorganic fertilizers. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

July 1986 to February 1989 shrubs were not fertilized. Of importance is that leaves of *P. neriifolia* have a long lifespan with approximately 83% of the leaves originally tagged still present after 12 months, 52% still present after 24 months, and 40% present after 32 months. This relatively long leaf lifespan in cultivated *P. neriifolia* is supported by casual observations by the author of ten year old leaves on cultivated *P. neriifolia*. Similarly, six to ten year old leaves have been observed on young (ten year old) *P. neriifolia* growing in its natural habitat, the southern Cape Province of South Africa (Personal communication, J.P. Rourke, Compton Herbarium, National Botanic Gardens, Kirstenbosch, Private Bag X7, Claremont, 7735, South Africa).

There is an interesting difference in co-occurring, fire-protected *P. roupelliae* and *P. caffra*, two proteas naturally occurring at the study site. Casual observations show a long leaf lifespan for *P. roupelliae* (up to five years), whereas *P. caffra* can be described as deciduous, with an annual production and loss of leaves ie. leaf lifespan of only one year. However, *P. roupelliae* regenerates by reseeding while *P. caffra* is a rootstock regenerator, and the two are known to have different leaf shedding strategies (Rourke, personal communication).

3.2 Shrub phenology

3.2.1 Shoot growth and flowering

A summary of shoot growth, phenology and flower production of cultivated *P. neriifolia* for the periods 1984/1985, 1985/1986 and 1986/1987 is presented in Table 3.3. As a mean, of the 100 primary shoots initially tagged, 33% remained vegetative, 62% became reproductive and the remaining 5% died. The mean annual growth of primary shoots was 144 ± 20 mm and a mean number of lateral shoots of 1.4 was produced from each primary shoot. The mean annual growth of the lateral shoots was greater than that for primary shoots viz. 170 ± 18 mm. The mean total annual growth of primary and lateral shoots was 383 ± 69 mm with, during 1984/1985 and 1985/1986, lateral shoots contributing more to total growth

Table 3.3 Comparison of phenological characteristics and growth data of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers.

	Jul 84 - Jun 85	**Jul 85 - Jun 86**	**Jul 86 - Jun 87**
% primary shoots remaining vegetative	28	28	44
% primary shoots becoming reproductive	67	62	56
% primary shoots dead	5	10	0
Mean no of lateral shoots per primary shoot	1.51	1.96	0.72
Mean annual growth - primary shoots (mm)	176	111	145
Standard deviation	26	16	17
Mean annual growth - lateral shoots (mm)	174	171	165
Standard deviation	22	22	18
Total annual growth per primary shoot (mm) (primary and lateral shoots)	439	446	264
Mean no of flowers per shrub per year	18.1	37.7	16.4
Standard deviation	1.2	2.8	1.6
Mean dry mass loss per shrub per year (kg)*	0.9	1.8	1.1
Standard deviation	0.07	0.09	0.09

Note: although secondary lateral shoots (lateral shoots from lateral shoots) were produced, they were limited in number and have not been included in the above data set.

* dry mass loss as a result of the harvesting of flowers.

than the primary shoots originally tagged. The greater contribution of lateral shoots than primary shoots to total growth is as a result of the cessation of the growth of the primary shoot when the terminal flower bud is set. The mean annual number of flowers produced per shrub was 24.1 ± 5.9.

Comparisons between the three periods show that during 1984/1985, primary shoots grew more than in either 1985/1986 or 1986/1987. Statistical analysis shows these differences are statistically significant. Similarly, lateral shoots produced in 1984/1985 grew more than in either 1985/1986 or 1986/1987 although statistical analysis shows that these differences were not statistically significant. However, analysis of variance and a multiple range test did show that the number of lateral shoots produced per primary shoot in 1986/1987 was significantly lower than in the previous two periods. This was probably the result of a severe hailstorm in December 1986 (Section 2.1.2) with lateral buds being either damaged or killed. This hailstorm would also account for the low total growth recorded for the 1986/1987 period and the relatively high standard deviation recorded above for the mean total annual growth for the three periods. The effects of the hailstorm are also shown in the mean annual flower production per shrub. From 1984/1985 to 1985/1986 there is a doubling in the number of flowers produced per shrub. This was expected with the increase in shrub age and size. However, flower production per shrub in 1986/1987 was less than that for 1984/1985 despite the shrubs being two years older. The hailstorm occurred in December 1986, at the time that flower buds are set or are being set (Heinsohn and Pammenter, 1988) and it is likely that flower buds were damaged or killed and as a result did not develop further. This trend is also shown by dry mass loss as a result of flower harvesting (Table 3.3).

For each of the three seasons, peak vegetative growth (primary and lateral shoots combined) occurred in September (early spring) with summer (December, January and February) growth rates being only slightly higher than in autumn (March, April and May) or winter (June, July and August) (Figure 3.4). Flowering occurred from January to July with the maximum

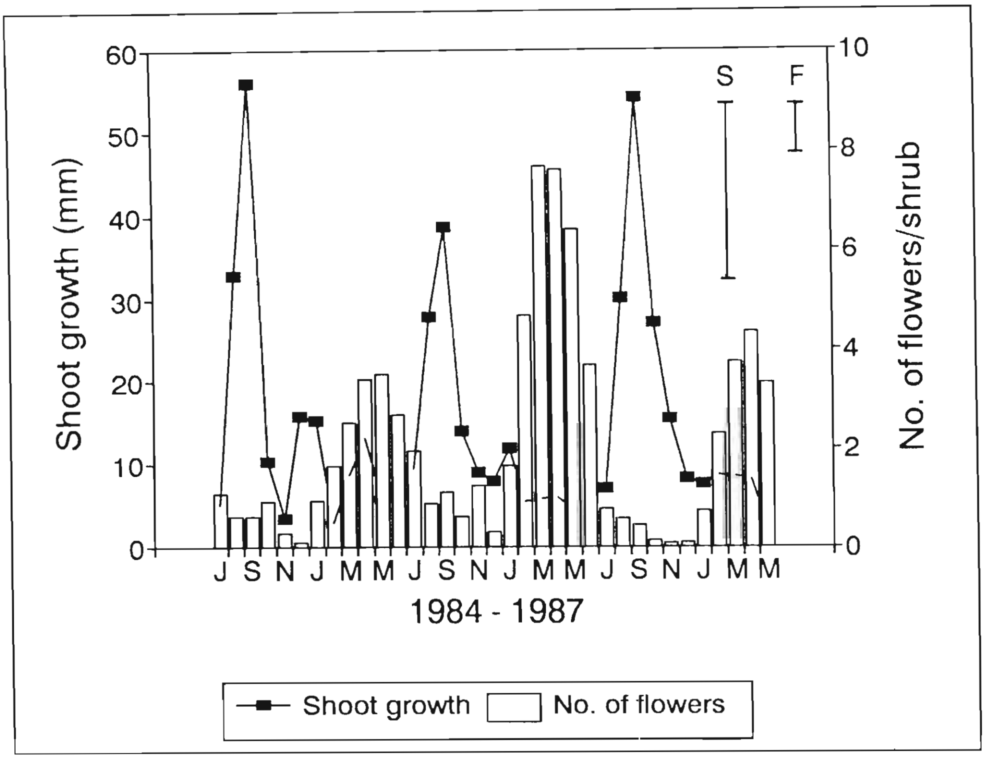


Figure 3.4 Mean monthly extension growth of primary and lateral shoots combined, and mean number of flowers harvested per month per shrub from *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The minimum significant difference ($P \leq 0.05$) for shoot growth (S) and flowers harvested (F), is given by the two isolated bars. Differences that are greater than the MSD are statistically significant.

yield of commercially harvestable flowers in March, April and May (autumn) ie. at a time when active vegetative growth is lowest (Figure 3.4).

Extension growth of primary shoots (those that remained vegetative and those that became reproductive) showed peak growth in September (early spring) of any year (Figure 3.5). Extension growth of lateral shoots produced from vegetative and reproductive primary shoots also showed peak growth in September (early spring) with a smaller peak in extension growth in December/January (summer) (Figure 3.6). This smaller peak in lateral shoot extension growth was more apparent during 1984/1985 and 1985/1986 than in 1986/1987. Again, this was probably as a result of the hailstorm experienced in December 1986.

For 1984/1985 and 1985/1986, the sprouting of lateral buds on vegetative primary shoots and reproductive primary shoots prior to the harvest of the flower was very variable (Table 3.4) and showed no seasonal patterns except for low rates during November - December, the peak period of flower bud formation (personal observation) and March - May, the peak flowering period (Figure 3.4). For 1986/1987, the sprouting of lateral buds followed a similar pattern to the previous two periods until the hailstorm in December 1986. Thereafter there was no lateral shoot production until April 1987. This accounts for the low numbers of lateral shoots per primary shoot recorded for the 1986/1987 period (Table 3.3).

3.2.2 Root growth

The dry mass of proteoid roots recovered from 100 g soil varied from 0.16g in May to 1.39g in October (Figure 3.7). A pattern of proteoid root seasonality is evident with maximum root biomass occurring between August to November (late winter/spring) and a decline from December to May

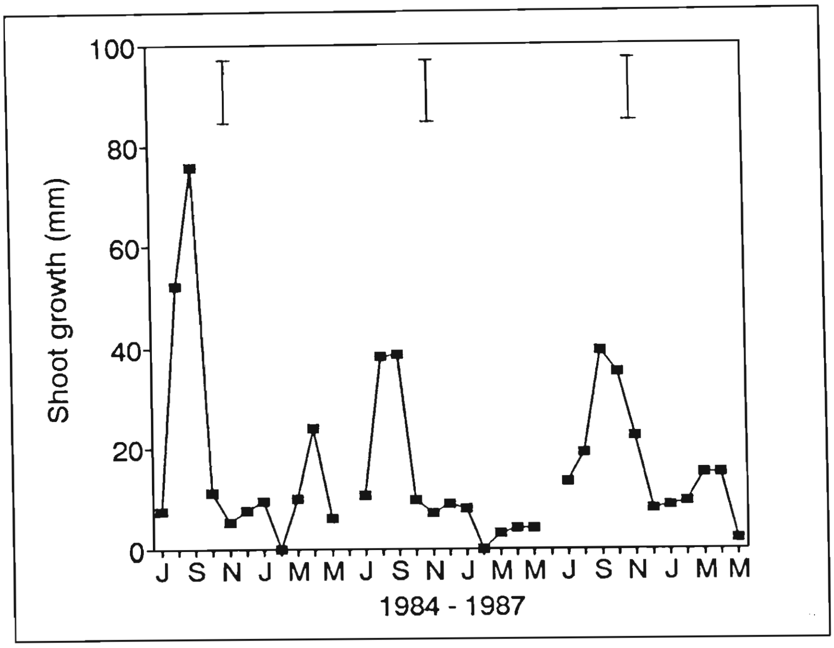


Figure 3.5 Mean monthly shoot growth of primary shoots of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar for each 11 month period represents the minimum significant difference (P $\leq$ 0.05). Differences greater than the MSD are statistically significant.

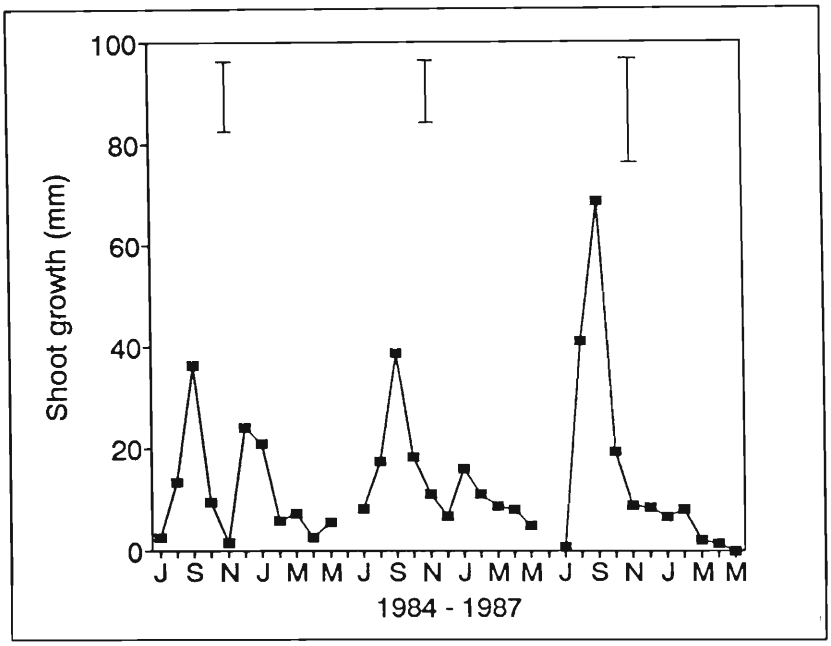


Figure 3.6 Mean monthly shoot growth of lateral shoots produced from primary shoots of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar for each 11 month period represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

Table 3.4 Monthly lateral shoot production from 100 primary shoots of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers.

			1984 - 1985	**1985 - 1986**	**1986 - 1987**
July	-	August	20	20	17
August	-	September	24	36	20
September	-	October	20	22	15
October	-	November	22	22	11
November	-	December	4	5	5
December	-	January	19	27	0
January	-	February	16	29	0
February	-	March	15	27	0
March	-	April	2	2	0
April	-	May	3	2	2
May	-	June	6	4	2
Total			151	196	72

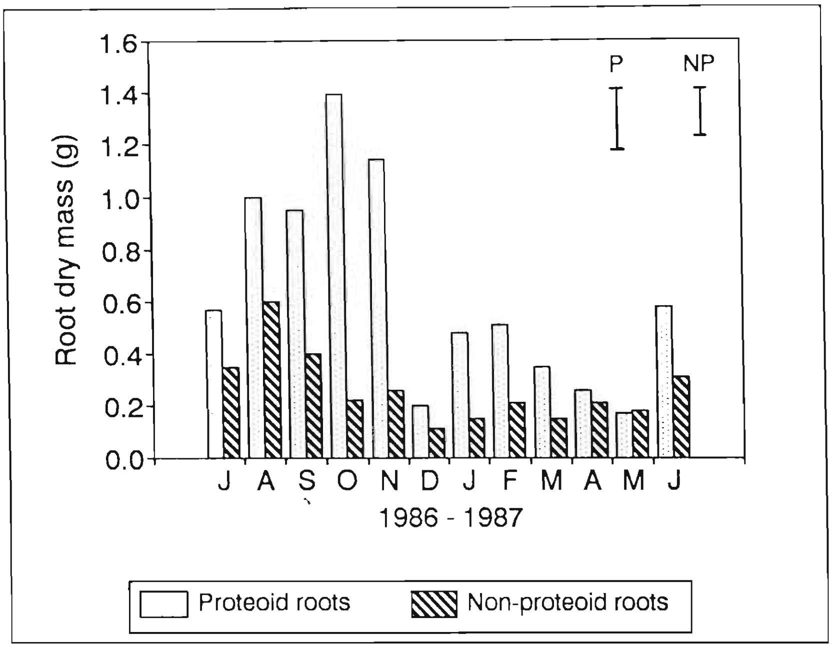


Figure 3.7 Seasonal variation in dry mass of proteoid and non-proteoid roots of *P. neriifolia* cultivated in a summer rainfall area. The vertical bar represents the minimum significant difference for proteoid (P) and non-proteoid (NP) roots ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

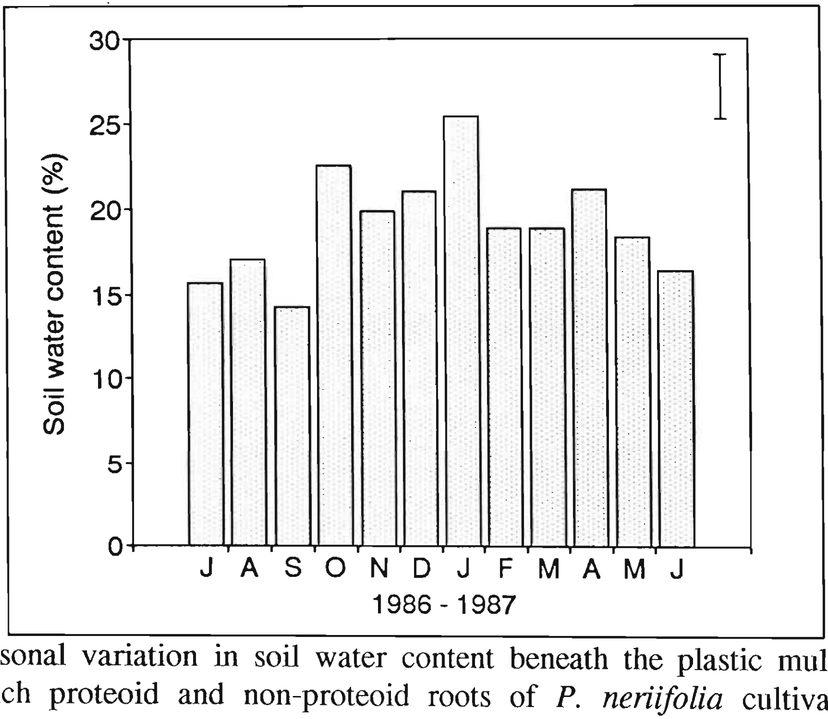


Figure 3.8 Seasonal variation in soil water content beneath the plastic mulch under which proteoid and non-proteoid roots of *P. neriifolia* cultivated in a summer rainfall area were sampled. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant. Field capacity of soils = 37.2% (n = 36).

(summer and autumn). This is followed by a slight increase in occurrence in June and July (winter) prior to the greatest peak described earlier. The MSD value presented in Figure 3.7 shows that the observed seasonal variation in proteoid root occurrence is statistically significant.

Soil moisture levels beneath the plastic mulch (Figure 3.8) varied from a low (14%) in September (early spring) to a high (26%) in January (summer) reflecting the seasonal rainfall pattern of the area (Figures 2.4 and 2.5).

Non-proteoid roots also showed slight seasonal variation in occurrence with a peak between June and September (winter/early spring) slightly preceding and co-incident with the peak in proteoid root occurrence (August to November) (late winter/spring) (Figure 3.7). Again, the MSD calculated for non-proteoid root occurrence shows that this seasonal variation is statistically significant.

In summary, therefore, both proteoid and non-proteoid roots exhibit greatest occurrence during the winter/early spring months. Root production is initiated prior to an increase in soil moisture (October to January) although soil moisture throughout the year is never very low.

3.3 Litter production and decomposition

3.3.1 Litter production

Highest values of shrub litter production were recorded in August (late winter) of each year with distinct seasonal variations in litter loss throughout the year (Figure 3.9). Peak litter production occurs between May and December (late autumn to early summer) with a decline between January and April (summer to autumn). This peak in litter production coincides with the period in which shrub leaf area also declines (Figure 3.2). Statistical analysis shows this seasonal trend in litter production to be significant. Leaf litter was found to contribute over 90% of the total litter in each month.

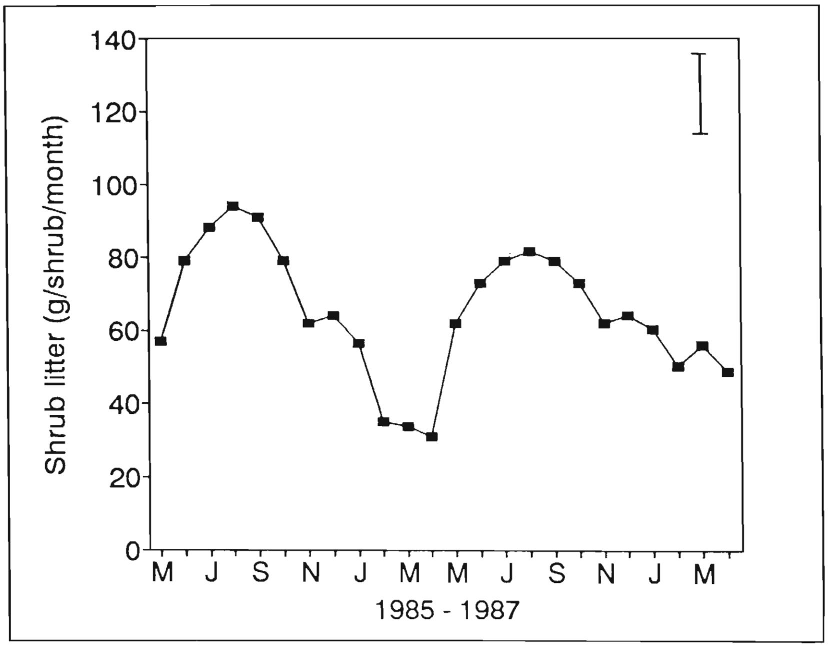


Figure 3.9 Seasonal variation in total litter production from *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

This is consistent with findings for *P. repens* litter composition (Mitchell and Coley, 1987).

Nutrient loss values were obtained by multiplying litter production for a period with litter nutrient concentration for the same period. The loss of nitrogen through litter production showed slight variation (Figure 3.10a) with peak nitrogen loss occurring between July and September (winter/early spring). Nitrogen loss throughout the rest of the year appears relatively constant. Both phosphorus (Figure 3.10b) and potassium (Figure 3.10c) loss through litter production showed a more marked peak loss period of July to September (winter/early spring) with little variation throughout the rest of the year.

MSD values in the respective figures show that seasonal variations are statistically significant and, therefore, nitrogen, phosphorus and potassium all show peak loss periods in accordance with peak loss periods of litter material itself. However, the nitrogen loss curve is flatter than that for total litter loss, indicating variation in litter nitrogen concentration during the period in which measurements were taken. There was no similar variation in litter phosphorus and potassium concentrations.

3.3.2 Litter decomposition

Rates of initial leaf litter decomposition (first three months) did not show seasonal variation throughout the year (Figure 3.11). The rate varied from a low of 11.6 mg g^{-1} day^{-1} in July (winter) to a high of 16.4 mg g^{-1} day^{-1} in October (spring) but statistical analysis shows these differences not to be significant.

Decomposition followed over a period of 487 days showed a relatively high decomposition rate of 15.2 mg g^{-1} day^{-1} for the first 60 days, followed by a sharp decline to 7.3 mg g^{-1} day^{-1} in the following 60 days (Figure 3.12a). Decomposition rate declined further to a lowest rate of 1.3 mg g^{-1} day^{-1} after

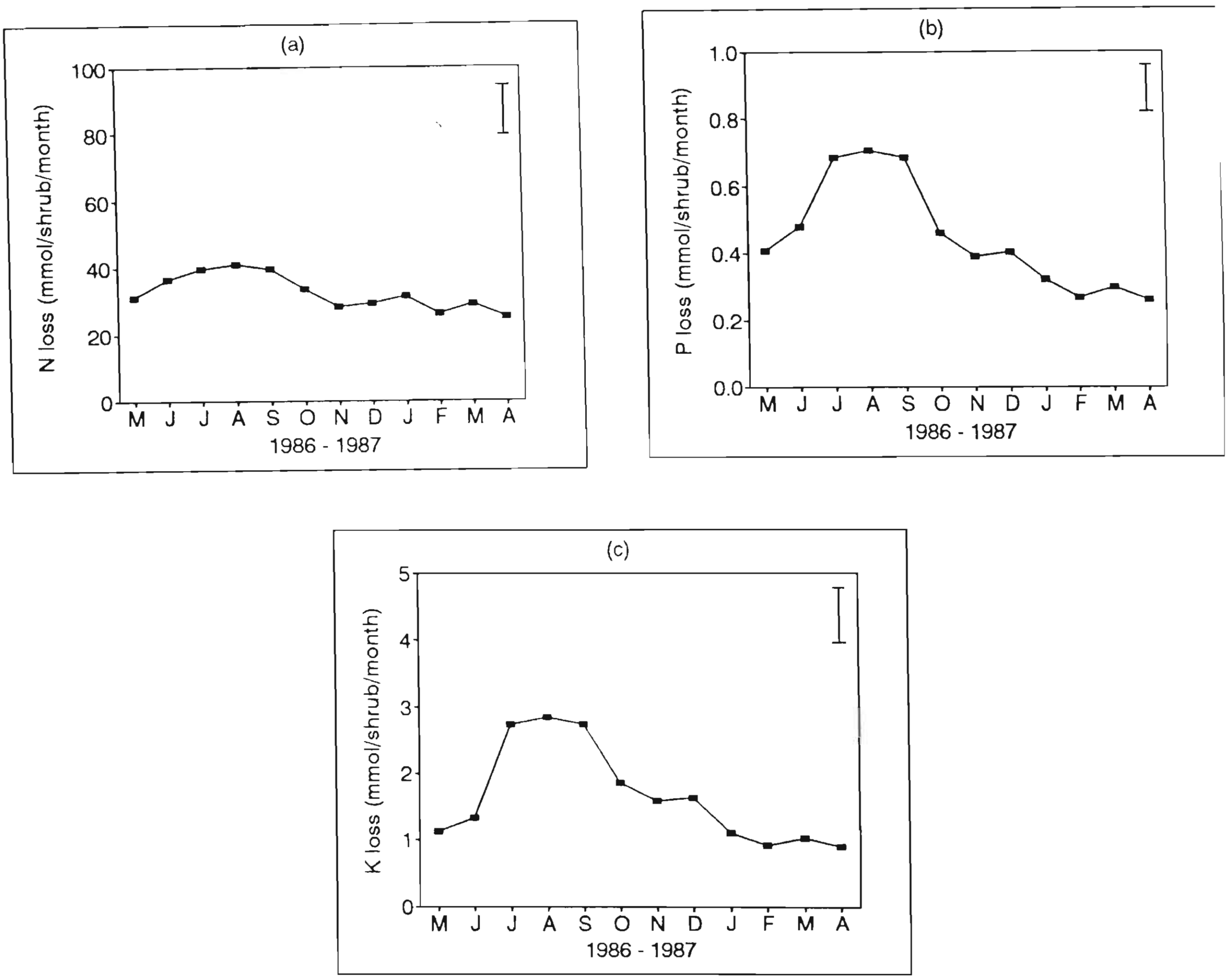


Figure 3.10 Seasonal variation in total (a) nitrogen, (b) phosphorus, and (c) potassium loss in the litter from *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

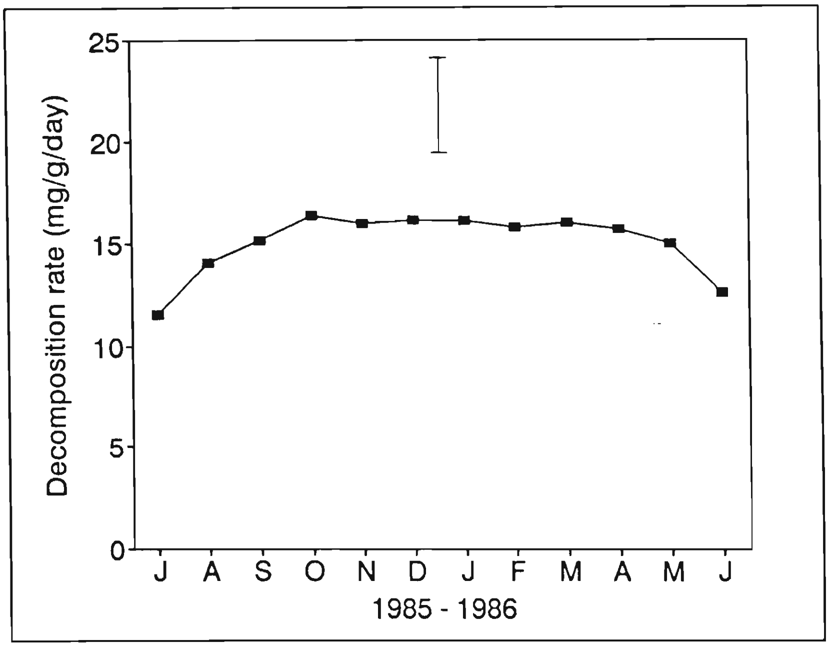
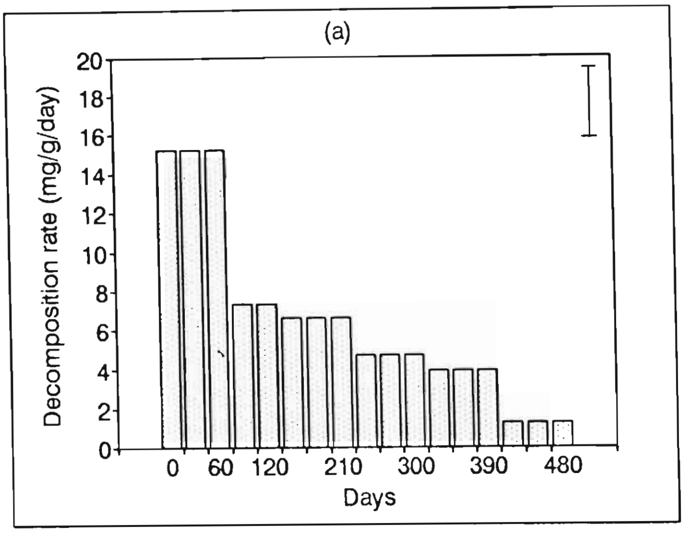


Figure 3.11 Seasonal variation in initial decomposition rate of leaf litter of *P. neriifolia* cultivated in a summer rainfall area. Three litter bags were placed in the field each month for one year. These bags were retrieved after three months and decomposition rates for this three month period were calculated. Monthly values are the means of nine replicates representative of decomposition rates for each particular month. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.



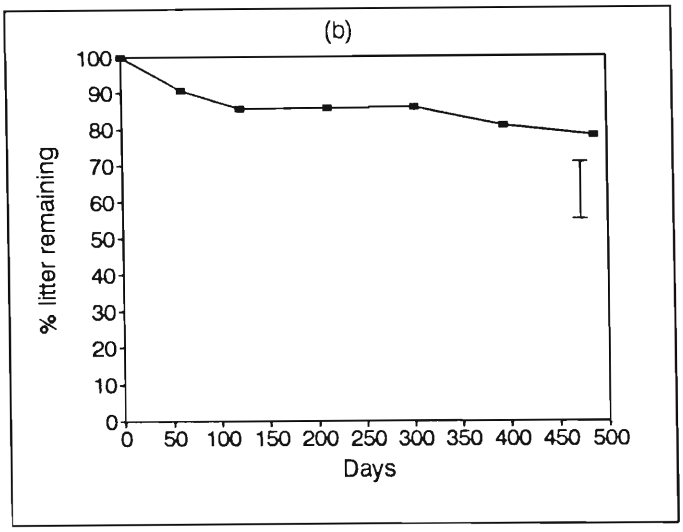


Figure 3.12 (a) rate of litter decomposition and (b) % litter remaining for *P. neriifolia* cultivated in a summer rainfall area. Litter bags were placed in the field in August 1984 and ten bags were retrieved at regular intervals until December 1985. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

487 days. MSD calculations show that differences in the decomposition rate with time are statistically significant. However, these decomposition rates are relatively slow as shown by the high percentage of litter remaining after 487 days (Figure 3.12b). In the first 60 days approximately 10% of leaf litter is decomposed while after 487 days only 22% of leaf litter has been decomposed with 78% of the original leaf litter remaining. This is supported by the casual observation of leaf litter accumulation beneath mature *P. neriifolia* shrubs.

The slow decomposition rate of leaf litter is accompanied by slow release of nitrogen, phosphorus and potassium (Figure 3.13a, b and c). Leaf litter nitrogen concentration shows a slow decline from 0.5 mmol g^{-1} after 60 days to 0.3 mmol g^{-1} after 487 days (Figure 3.13a). Similarly, phosphorus concentration declines from 0.006 to 0.004 mmol g^{-1} (Figure 3.13b) and potassium concentration from 0.011 to 0,009 mmol g^{-1} (Figure 3.13c) for the same time periods.

Fresh leaf litter contains mean nitrogen, phosphorus and potassium concentrations of 0.56 mmol g^{-1}, 0.009 mmol g^{-1} and 0.031 mmol g^{-1}, respectively. Nitrogen (Figure 3.14a), phosphorus (Figure 3.14b) and potassium (Figure 3.14c) are released at the highest rate during the first 60 days. During the remaining period (61 - 487 days), nutrient release rates for each of the three nutrients were considerably lower. This pattern of nutrient release is more marked for phosphorus and potassium than for nitrogen. There is a rise in nitrogen release rate during the 304 - 395 day period. The release rate during this period (0.736 μmol g^{-1} day^{-1}) was comparable to the nitrogen release rate in the first 60 days (0.967 μmol g^{-1} day^{-1}). No explanation for this increase could be found. In each case, however, nutrient return over a longer period is slow with much nutrient still bound within the leaf litter after 15 months. MSD calculations show that observed differences in release rates for each of the three nutrients are statistically significant ($P \leq 0.05$).

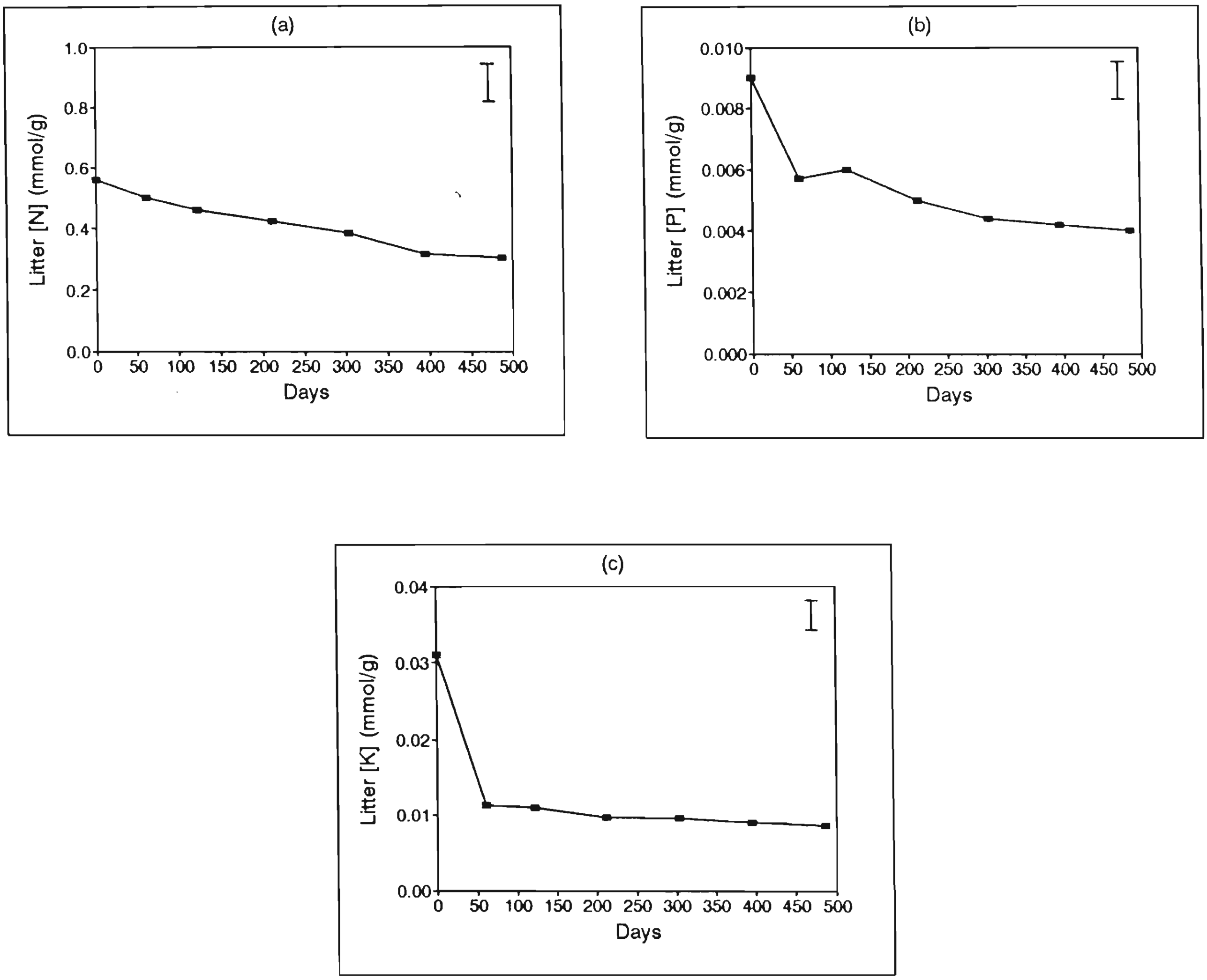


Figure 3.13 Leaf litter (a) nitrogen, (b) phosphorus, and (c) potassium concentration after decomposition for various lengths of time. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are significantly different.

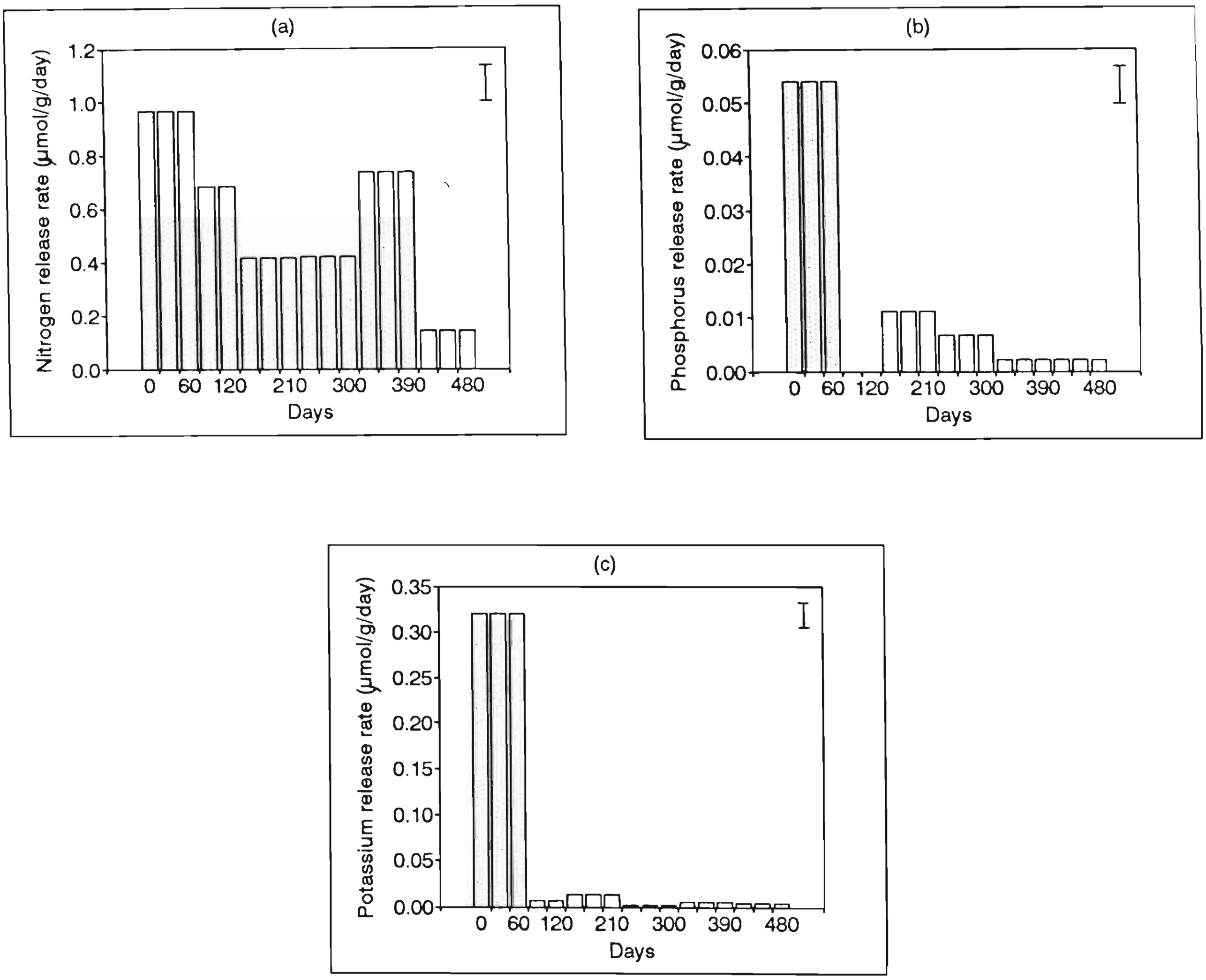


Figure 3.14 Release rates of (a) nitrogen, (b) phosphorus, and (c) potassium from decomposing litter of *P. neriifolia* cultivated in a summer rainfall area. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

3.4 Nutrient status

3.4.1 Shrub nutrient status

Variations in (a) leaf and stem, and (b) floret and bract nitrogen concentration during 1986/1987 are illustrated in Figure 3.15a and b. Both leaf and stem nitrogen concentration showed a peak between May and August (late autumn/winter) with lower levels during November and February (late spring/summer) (Figure 3.15a). MSD values show that observed seasonal variations in leaf and stem nitrogen concentration are statistically significant. In contrast, both floret and bract nitrogen concentration showed a peak between August and November (late winter/spring) with reduced levels during February to May (late summer/autumn) (Figure 3.15b). However, MSD values show that these differences are not statistically significant and that floret and bract nitrogen concentrations are of a similar level irrespective of the season.

Leaf and stem phosphorus concentrations showed a similar seasonality to that of leaf and stem nitrogen concentration viz. a peak between May and August (late autumn/winter) with reduced levels during November and February (late spring/summer) (Figure 3.16a). Again, statisitical analysis shows seasonality in leaf and stem phosphorus concentrations to be significant. Although floret and bract phosphorus concentrations do show some variation with season (Figure 3.16b), MSD values calculated show that these differences are not statistically significant. Therefore, as with floret and bract nitrogen concentration, floret and bract phosphorus concentrations do not vary seasonally.

Leaf and stem potassium concentrations showed little variation seasonally with highest levels recorded in May (late autumn) and lowest levels recorded in November (late spring) (Figure 3.17a), variations supported by statistical analysis. Floret and bract potassium concentrations showed very little

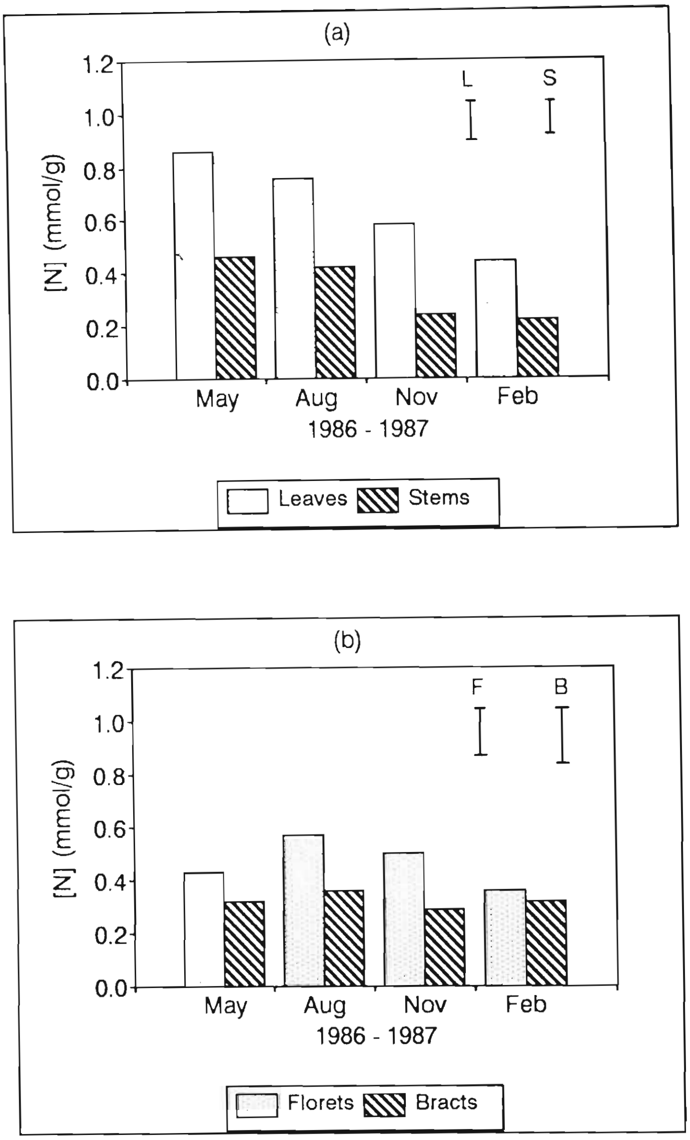
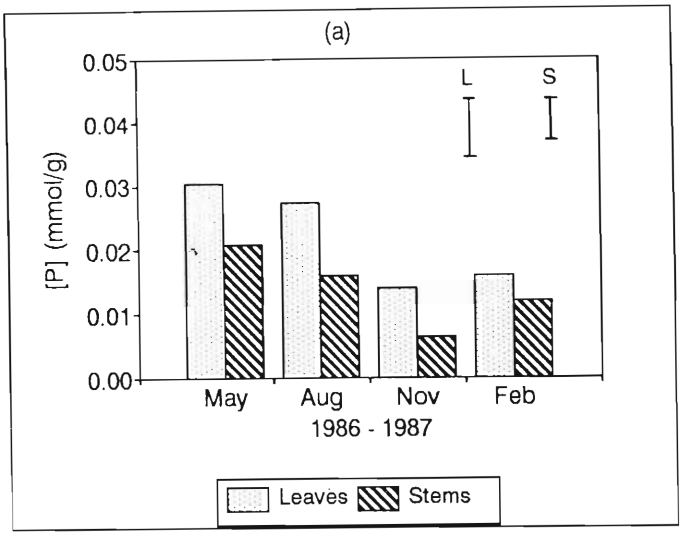


Figure 3.15 Seasonal variation in nitrogen concentration in (a) leaves and stems, and (b) florets and bracts of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar in each case represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.



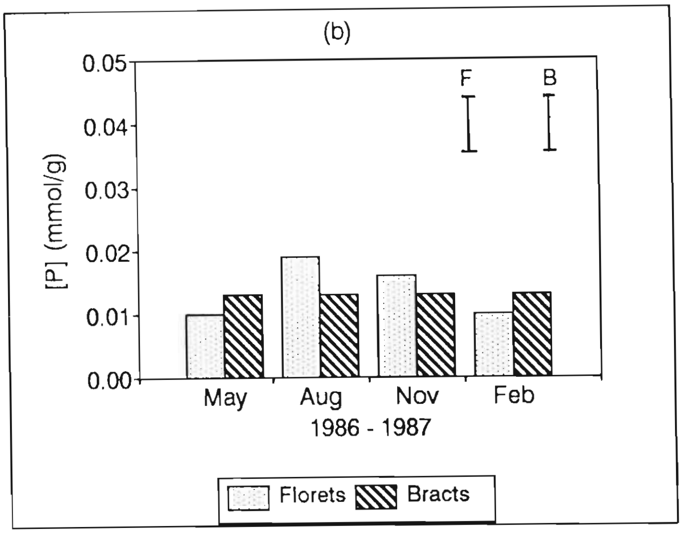


Figure 3.16 Seasonal variation in phosphorus concentration in (a) leaves and stems, and (b) florets and bracts of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar in each case represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

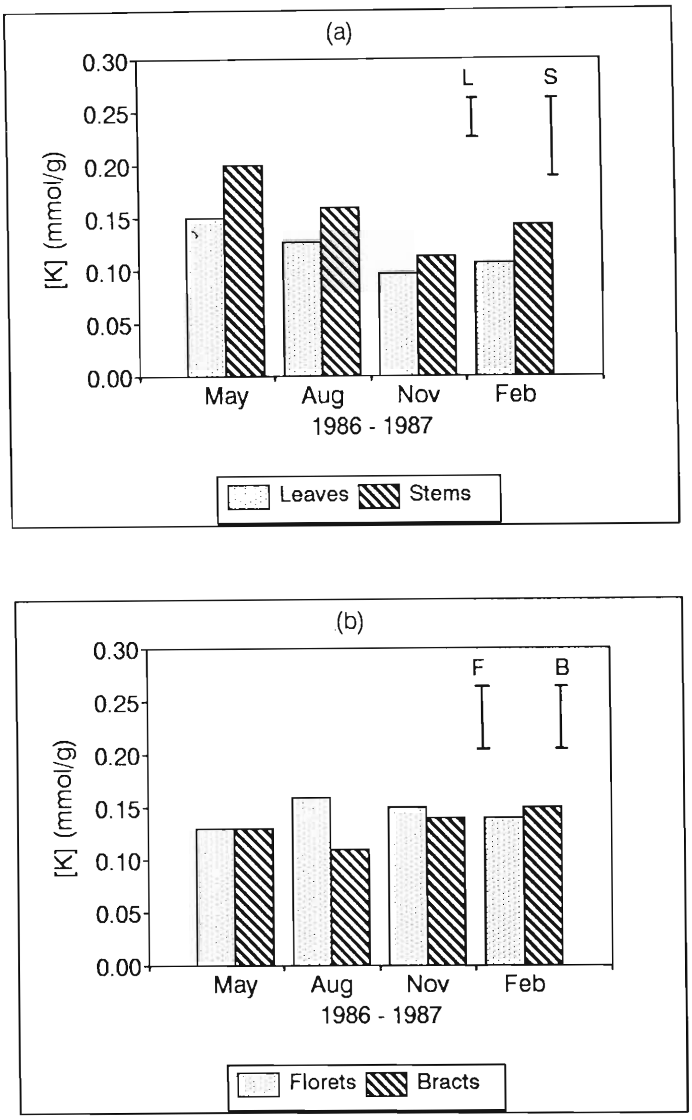


Figure 3.17 Seasonal variation in potassium concentration in (a) leaves and stems, and (b) florets and bracts of *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The vertical bar in each case represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

variation throughout the year (Figure 3.17b), again supported by statistical analysis. From data illustrated in Figures 3.17a and b it is likely that potassium concentrations do vary during the year but data do not support that this variation is directly related to seasons.

In summary, therefore, leaf and stem nitrogen and phosphorus concentrations are highest in late autumn/winter when new vegetative growth is initiated. Similarly, floret and bract nitrogen concentration are greatest in late winter/spring when new reproductive growth is initiated. Floret and bract phosphorus concentration did not vary seasonally and it is unlikely that potassium concentration in any of the shrub parts varies seasonally. Where seasonal variation did occur, it was unlikely that this was due to shrub age. This is because at each sampling only the newest plant tissues were analysed (Section 2.3.1).

The nutrient status of proteoid and non-proteoid roots was not measured for the 1986/1987 period. A sampling for the 1988/1989 period was initiated and although prematurely halted by the death of the shrubs, the mean nitrogen, phosphorus and potassium concentrations for unfertilized *P. neriifolia* shrubs for the two sample periods (November 1988 and February 1989) are presented in Table 3.5. Proteoid root nitrogen concentration was comparable to that of other shrub parts described above, while non-proteoid root nitrogen concentration was considerably lower (half that of proteoid roots). Similarly, proteoid root phosphorus concentration was comparable to other shrub parts while non-proteoid root phosphorus concentration was considerably lower. Again, proteoid root phosphorus concentration was double that of the non-proteoid roots. Both proteoid and non-proteoid root potassium concentrations were similar although considerably less than potassium concentrations for other shrub parts (up to 60% less than potassium concentrations in stems).

Table 3.5 Nitrogen, phosphorus and potassium concentration of proteoid and non-proteoid roots of *P. neriifolia* cultivated in a summer rainfall area without the addition of inorganic fertilizers. Values are the means (± one standard deviation) of 10 replicates.

	Proteoid roots (mmol g^{-1})	**Non-proteoid roots (mmol g^{-1})**
Nitrogen	0.6020 ± 0.2200	0.2990 ± 0.1300
Phosphorus	0.0105 ± 0.0020	0.0045 ± 0.0010
Potassium	0.0595 ± 0.0020	0.0540 ± 0.0090

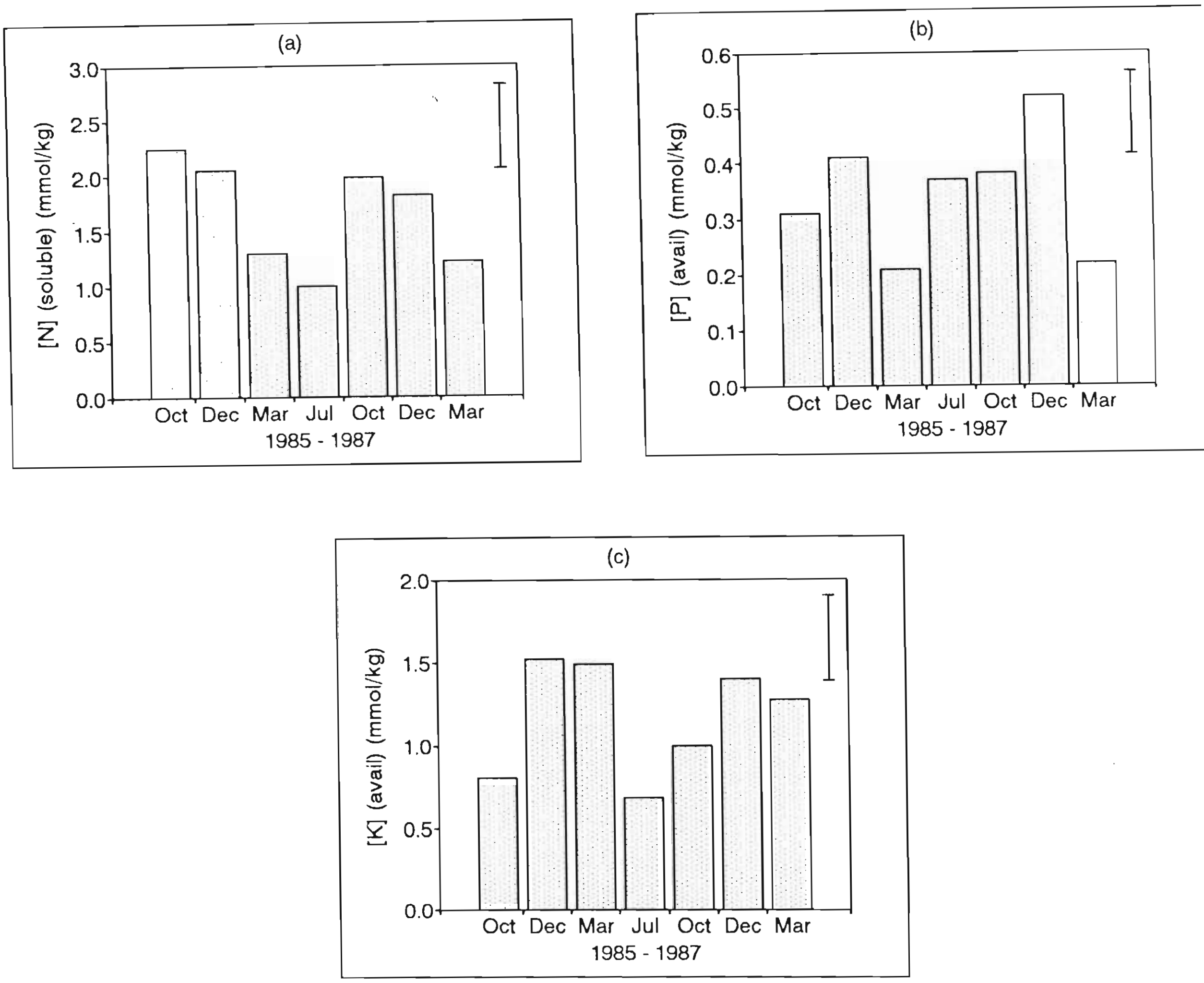


Figure 3.18 Seasonal variation in (a) soluble nitrogen, (b) available phosphorus, and (c) available potassium of the soils of the MSNR study site prior to the application of inorganic fertilizers. The vertical bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

3.4.2 Soil nutrient status

The mineral status of soils in which *P. neriifolia* was cultivated prior to the addition of inorganic fertilizers was shown in Table 2.1 and discussed in Section 2.1.2. The soils are well drained and highly leached and, for the range of minerals analysed, are of a low nutrient status, comparable to strongly leached heathlands, for example, fynbos.

Values presented in Table 2.1 are the means of 105 replicates sampled at three monthly intervals over 1.5 years. If the data are viewed for the various sample periods, soluble nitrogen, available phosphorus and available potassium showed seasonality in concentration (Figure 3.18a, b and c). Soluble nitrogen is greatest between October and December (spring/early summer) and lowest between March and July (autumn/winter) (Figure 3.18a). Available phosphorus showed the highest concentration between July and December (winter/spring/early summer) and a low during March (early autumn) (Figure 3.18b), while available potassium showed the highest concentration between December and March (summer/early autumn) and the lowest concentration between July and October (winter/spring) (Figure 3.18c). Therefore, for both soluble nitrogen and available phosphorus, concentrations are greatest during spring and summer (wet season) while available potassium concentration is greatest slightly later in the season, summer to autumn (wet to dry season).

Minimum significant difference values for soil nutrient concentrations are relatively large because data are variable. Nevertheless, in each case, MSD values do show differences to be statistically significant supporting observed seasonality in soil soluble nitrogen, available phosphorus and available potassium concentrations.

3.4.3 The chemical composition of rainwater, shrub throughfall, stemflow, and stream-water

In Section 2.4.3 the reasons for limited data on the chemical composition of rainwater, shrub throughfall, stemflow and stream-water are given. However, the above were measured for two periods, November 1988 and February 1989, and the mean nitrogen, phosphorus and potassium concentrations for unfertilized *P. neriifolia* for the two sample periods are presented in Table 3.6. Soil-water runoff was not collected. Rather, stream-water was collected and analysed. Therefore, in this thesis stream-water is taken to include soil-water runoff, both directly from the soil surface, and soil-water that leaches to the impermeable rock layer and then flows into the stream-water.

The concentration of nitrogen (57.1 μmol l^{-1}) in rainwater was considerably higher than both the concentration of phosphorus (1.3 μmol l^{-1}) and potassium (17.9 μmol l^{-1}). Shrub throughfall patterns were, however, different. For both phosphorus (3.1 μmol l^{-1}) and potassium (60.1 μmol l^{-1}), throughfall concentrations were greater than concentrations in rainfall. Similarly, phosphorus and potassium concentrations in shrub stemflow were greater than in the rainwater. Since throughfall and stemflow include dry matter fallout washed from shrubs during rainfall, increases in phosphorus and potassium were due to either dry matter washing or leaching of nutrients from the shrubs. Although the nitrogen concentrations in rainwater, throughfall and stemflow were not significantly different, when calculated for the nutrient budget, the observed reduction in nitrogen concentration in shrub throughfall and stemflow compared with rainwater did imply a slight absorption of nitrogen by the shrub canopy, and this is included in the nitrogen budget. Stream-water analysis showed nitrogen levels (50.0 μmol l^{-1}) to be slightly less than the nitrogen concentration in rainfall. Stream-water phosphorus concentration (3.1 μmol l^{-1}) was greater than rainwater phosphorus concentration (1.3 μmol l^{-1}). Since runoff to the stream-water accounts for only 31.8% of rainfall, it would appear that some leaching of phosphorus from the soil (or parent rock) may occur. There does

Table 3.6 The chemical composition of rainwater, shrub throughfall, stemflow, and stream-water for unfertilized *P. neriifolia* cultivated in a summer rainfall area. Values are the means (± one standard deviation) of November 1988 and February 1989 samples replicated as described in Section 2.4.3.

Sample type	**Nitrogen (μmol l^{-1})**	**Phosphorus (μmol l^{-1})**	**Potassium (μmol l^{-1})**
Rainwater	57.1 ± 20.40	1.3 ± 0.02	17.9 ± 0.70
Shrub throughfall	42.8 ± 16.80	3.1 ± 0.78	60.1 ± 7.50
Shrub stemflow	48.8 ± 18.30	3.0 ± 0.86	59.2 ± 6.90
Stream-water	50.0 ± 4.20	3.1 ± 0.38	17.9 ± 0.90

not appear to be any soil potassium leaching during rainfall as stream-water and rainwater concentrations were equal.

3.5 Nutrient cycling and budgets

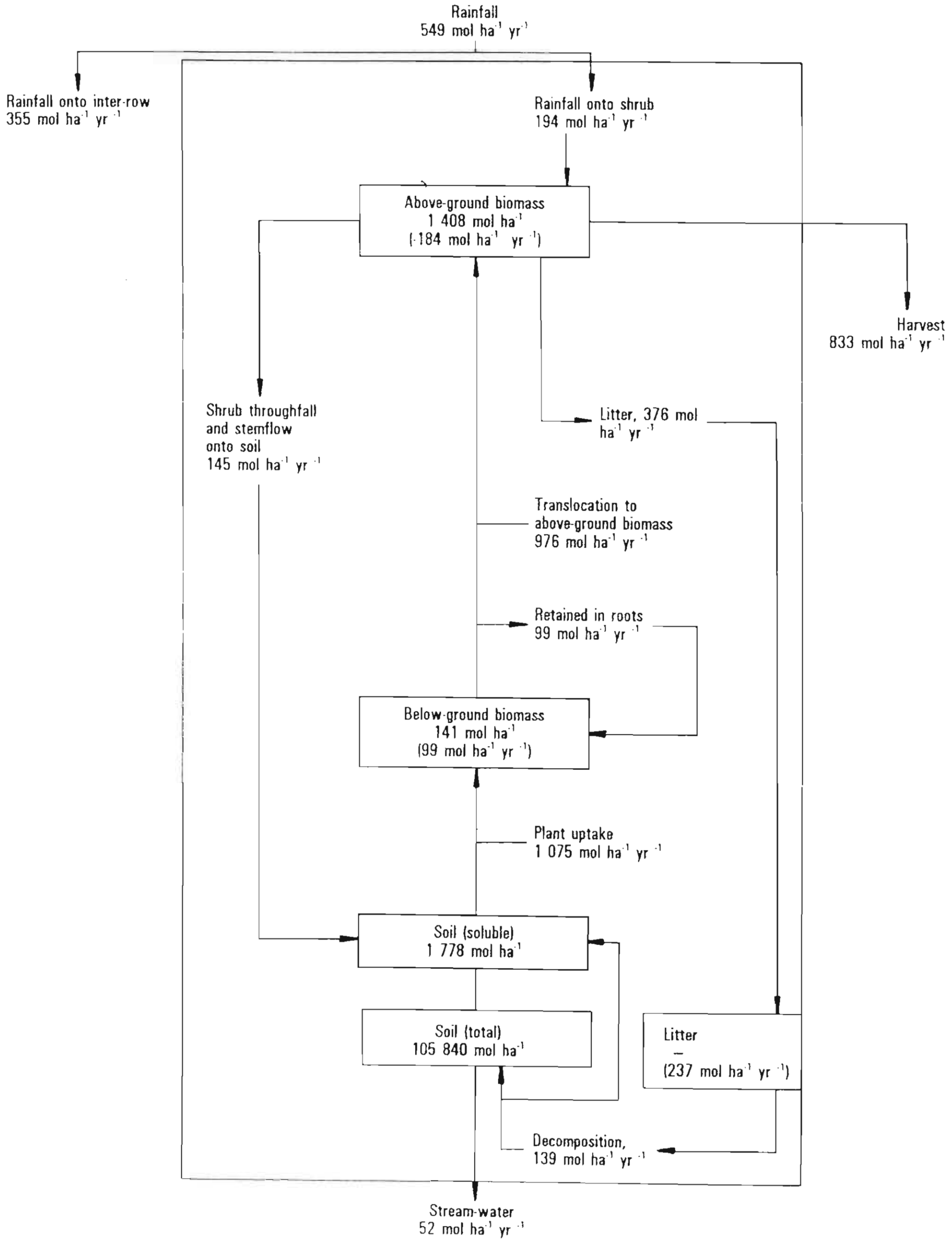
The nutrient cycling flows and annual budgets for nitrogen, phosphorus and potassium for seven year old unfertilized *P. neriifolia* cultivated in a summer rainfall area are illustrated in Figures 3.19a, b and c, respectively. Data presented in the annual budgets were obtained from the preceding presentation of results and are presented on an hectare basis assuming a standard planting density of 1 000 shrubs per hectare (Section 2.1.3). Pool sizes are expressed as mol ha^{-1} and fluxes as mol ha^{-1} yr^{-1}. Annual increments in pool sizes, shown in parentheses, are also expressed as mol ha^{-1} yr^{-1}. It is important to note that although budgets are expressed on an hectare basis, the budgets refer to the protea component only ie. budgets do not include the grass and for communities that occurred between the rows in which the shrubs were cultivated.

In each case the major nutrient pools are in the above- and below-ground biomass, the soil (soluble), the soil (total), and in the litter. Whole shrub dry mass for 1986 and 1987 is presented in Table 3.1. Shrub component dry masses for 1986 are illustrated in Figure 3.1. Using Figure 3.1, above- and below-ground biomass for 1986 could be calculated.

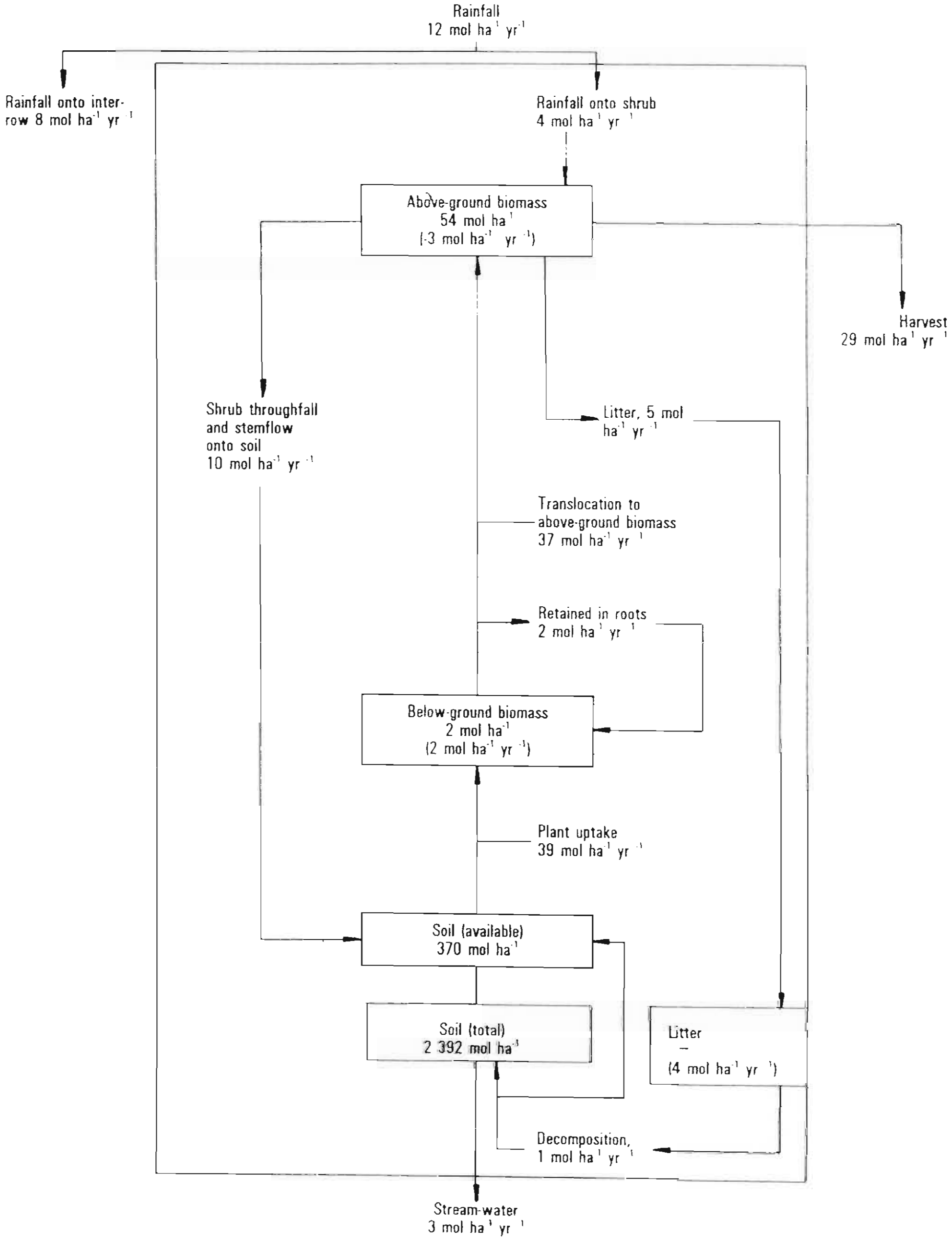
Similarly, using whole shrub dry mass data for 1987 (Table 3.1) and the same percentage contribution of components to total shrub dry mass as measured in 1986 (Figure 3.1), above- and below-ground biomass could be calculated for 1987. Nutrient pool sizes for 1986 were calculated using shrub nutrient concentration data for May 1986 to February 1987 presented in Figures 3.15, 3.16 and 3.17 and Table 3.5, and shrub component dry mass data presented in Figure 3.1. Nutrient pool sizes for 1987 were calculated using the same nutrient concentration data combined with component dry mass data, calculated as described earlier. The soil nutrient pool (available/soluble and total) is the respective mean value for the season (Table 2.1). For each nutrient, the mean value was converted to mmol per

Figure 3.19 Annual nutrient budgets (a) nitrogen, (b) phorphorus, (c) potassium for seven year old *P. neriifolia* cultivated in the summer rainfall area prior to the addition of inorganic fertilizers. (Nutrient pools are shown in boxes and the value below the nutrient pool name is the size of the particular nutrient pool. Values in parentheses are annual increments in nutrient pool size, and values on arrows are annual nutrient flux rates.)

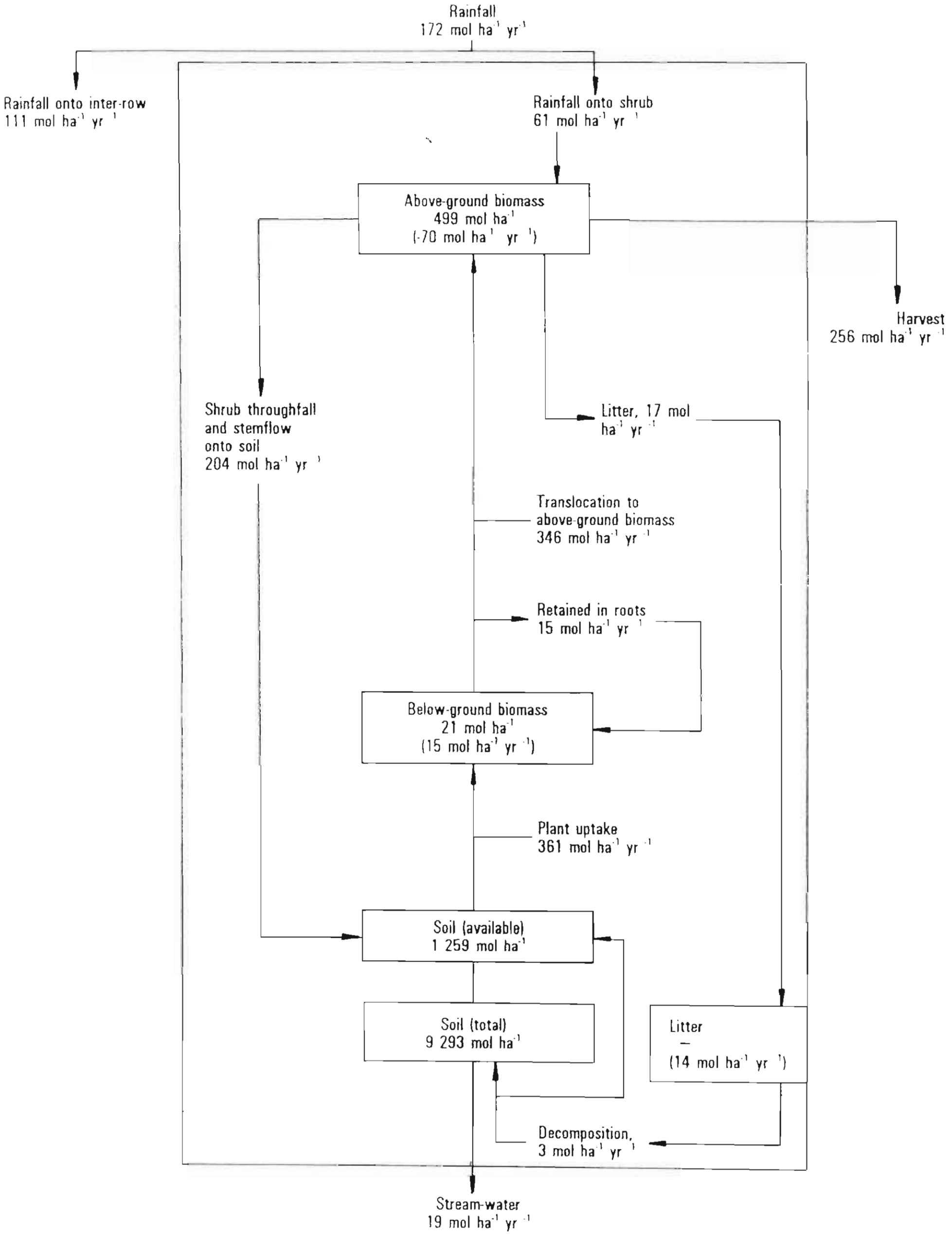
(a)


Rainfall
549 mol ha^{-1} yr^{-1}
Rainfall onto inter-row
355 mol ha^{-1} yr^{-1}
Rainfall onto shrub
194 mol ha^{-1} yr^{-1}
Above-ground biomass
1 408 mol ha^{-1}
(-184 mol ha^{-1} yr^{-1})
Harvest
833 mol ha^{-1} yr^{-1}
Shrub throughfall
and stemflow
onto soil
145 mol ha^{-1} yr^{-1}
Litter, 376 mol
ha^{-1} yr^{-1}
Translocation to
above-ground biomass
976 mol ha^{-1} yr^{-1}
Retained in roots
99 mol ha^{-1} yr^{-1}
Below-ground biomass
141 mol ha^{-1}
(99 mol ha^{-1} yr^{-1})
Plant uptake
1 075 mol ha^{-1} yr^{-1}
Soil (soluble)
1 778 mol ha^{-1}
Soil (total)
105 840 mol ha^{-1}
Litter
–
(237 mol ha^{-1} yr^{-1})
Decomposition,
139 mol ha^{-1} yr^{-1}
Stream-water
52 mol ha^{-1} yr^{-1}

(b)


Rainfall
12 mol ha⁻¹ yr⁻¹
Rainfall onto inter-row 8 mol ha⁻¹ yr⁻¹
Rainfall onto shrub
4 mol ha⁻¹ yr⁻¹
Above-ground biomass
54 mol ha⁻¹
(-3 mol ha⁻¹ yr⁻¹)
Harvest
29 mol ha⁻¹ yr⁻¹
Shrub throughfall and stemflow onto soil
10 mol ha⁻¹ yr⁻¹
Litter, 5 mol ha⁻¹ yr⁻¹
Translocation to above-ground biomass
37 mol ha⁻¹ yr⁻¹
Retained in roots
2 mol ha⁻¹ yr⁻¹
Below-ground biomass
2 mol ha⁻¹
(2 mol ha⁻¹ yr⁻¹)
Plant uptake
39 mol ha⁻¹ yr⁻¹
Soil (available)
370 mol ha⁻¹
Soil (total)
2 392 mol ha⁻¹
Litter
–
(4 mol ha⁻¹ yr⁻¹)
Decomposition,
1 mol ha⁻¹ yr⁻¹
Stream-water
3 mol ha⁻¹ yr⁻¹

(c)


Rainfall
172 mol ha^{-1} yr^{-1}
Rainfall onto inter-row
111 mol ha^{-1} yr^{-1}
Rainfall onto shrub
61 mol ha^{-1} yr^{-1}
Above-ground biomass
499 mol ha^{-1}
(-70 mol ha^{-1} yr^{-1})
Harvest
256 mol ha^{-1} yr^{-1}
Shrub throughfall
and stemflow
onto soil
204 mol ha^{-1} yr^{-1}
Litter, 17 mol
ha^{-1} yr^{-1}
Translocation to
above-ground biomass
346 mol ha^{-1} yr^{-1}
Retained in roots
15 mol ha^{-1} yr^{-1}
Below-ground biomass
21 mol ha^{-1}
(15 mol ha^{-1} yr^{-1})
Plant uptake
361 mol ha^{-1} yr^{-1}
Soil (available)
1 259 mol ha^{-1}
Soil (total)
9 293 mol ha^{-1}
Litter
–
(14 mol ha^{-1} yr^{-1})
Decomposition,
3 mol ha^{-1} yr^{-1}
Stream-water
19 mol ha^{-1} yr^{-1}

unit volume using the bulk density measured for the soil. Since the bulk of the roots of *P. neriifolia* occur in the top 200 mm of soil, soil samples were taken to this depth. Using this 200 mm depth it was possible to calculate the soil volume per hectare, and thus calculate the total concentration per hectare. This was done for both available/soluble and total soil nutrient pools. These three nutrient pools constitute the plant/soil system.

Nutrient pools in the litter were not measured because total litter fall could not be measured. However, increments in litter production were measured.

The major input into the system was from rainfall (Figure 2.4 and Table 3.6). Total rainfall input was calculated by multiplying the volume of rain (Figure 2.4) by the respective nutrient concentrations measured in rainwater (Table 3.6). The major loss from the system was due to the harvesting of flowers for the commercial flower market. Nitrogen, phosphorus and potassium loss were calculated by multiplying dry mass loss of flowers (Table 3.3) by the respective nutrient concentrations measured in the flowers (Figures 3.15, 3.16 and 3.17). This loss of nutrients included the loss of nutrients that occurred due to stem and leaf removal during flower harvesting. An additional loss of nutrients from the system occurred via stream-water, inclusive of soil nutrients that may be leached. This was calculated by multiplying the volume of stream-water (Section 2.4.3) by the respective nutrient concentrations measured in stream-water (Table 3.6). However, since a portion of rainfall was on to the inter-row and not available to the *P. neriifolia* shrubs (see below), only that portion of rainfall directly on to the shrubs was used for stream-water calculations.

There are three major nutrient flows within the system:

(a) rainfall, either directly on to the shrubs or on to the inter-row. Annual rainfall was converted to volume of rainfall. Using shrub canopy area (Table 3.1) it was possible to calculate the proportion of rainfall (Figure 2.4) that would fall on to the shrubs and on to the inter-row. These data were then multiplied by the respective nutrient concentrations (Table 3.6). Rainfall directly on to the shrubs results in throughfall of rainwater and stemflow. The levels of nutrients in throughfall and stemflow were obtained by multiplying the volume of each by the respective nutrient concentrations (Table 3.6). Nutrients in throughfall and stemflow enter the soil and, therefore, are available for uptake by the below-ground biomass. Nutrients in the rainfall on to the inter-row are probably used by the grass and for community and are, therefore, unavailable to the *P. neriifolia* shrubs. This portion of nutrients in the total rainfall is, therefore, not included in the budgets for the *P. neriifolia* shrubs.

(b) nutrients in litter produced were obtained from Figure 3.10. Nutrient release during litter decomposition was calculated using initial litter decomposition rates (Figure 3.11) and initial (0 - 60 days) nutrient release rates (Figure 3.14). It should be noted that the calculated release rate is a slight underestimate because there will be some nutrient release after the initial 60 day period, albeit small.

(c) nutrient uptake by the shrubs was calculated using a combination of the dry mass data presented in Table 3.1 and the shrub nutrient status data presented in Figures 3.15, 3.16 and 3.17 and Table 3.5. The difference in dry mass between 1986 and 1987, multiplied by the nutrient status of the shrub components, was taken as shrub uptake during the year. The calculation of the proportion of nutrients translocated to the above-ground biomass and that retained by the roots was performed using the same percentage contribution of components to total shrub dry mass, as measured in 1986 (Figure 3.1).

Annual increments in the nutrient pool sizes in the above- and below-ground biomass and in the litter were calculated from the budgets. For nutrient pools in the above-ground biomass, nutrient inputs were from rainfall and the soil. Outputs were from litter production, bush throughfall and stem flow, and the harvest of flowers. The difference between inputs and outputs was used as the annual increment. For nutrient pools in the below-ground biomass, nutrient inputs were from the soil. No nutrient outputs were measured and, therefore, the soil input was taken as the annual increment. Although no measure of the litter nutrient pool was made, inputs to the pool were from litter production, and outputs were due to litter decomposition and nutrient release. The difference between inputs and outputs was taken as the annual increment in the litter nutrient pool.

More nitrogen (Figure 3.19a) was cycled than potassium (Figure 3.19c) which in turn was greater than phosphorus (Figure 3.19b), illustrating the relative contribution of each of the nutrients to the vegetative and reproductive growth of the shrubs.

3.5.1 Nutrient pools

The nitrogen pool in the above-ground biomass is 3 times greater than the potassium pool and 26 times greater than the phosphorus pool. Similarly, the nitrogen pool in the below-ground biomass is 7 times greater than the potassium pool and 71 times greater than the phosphorus pool. Similarly, the soil pool of soluble N is 1.5 times greater than the available K pool and 5 times greater than the available P pool. This is comparable to the differences in the size of total soil pools. It is also interesting to note that for each nutrient, the total soil pool is greater than the available soil pool and greater than the above- and below-ground biomass pools. This greater concentration of nutrients in the above-ground biomass is similar to that which is found in nutrient-poor tropical systems, particularly when compared with the reverse situation in more nutrient-rich temperate ecosystems (Odum, 1971).

3.5.2 Inputs and losses

The only nutrient input into the system measured in this study was rainwater. Rainwater contained 3 times more nitrogen than potassium and 46 times more nitrogen than phosphorus (Figures 3.19a, b and c). Similarly, nitrogen loss through stream-water was 3 times greater than that for potassium but only 16 times greater than that for phosphorus. This suggests comparable leaching of nitrogen and potassium but a proportionately higher leaching of phosphorus. The proportional loss of phosphorus from the system through soil leaching is almost three times that of nitrogen and twice that of potassium.

The major source of nutrient loss from the cultivated *P. neriifolia* system is via the harvest of flowers for commercial sale. The annual nitrogen loss is 833 mol ha^{-1} which is 3 times greater than the annual potassium loss of 256 mol ha^{-1} and 29 times greater than the annual phosphorus loss of 29 mol ha^{-1}. The proportion of the loss rates of the three nutrients through flower harvesting closely reflect the proportion of the three nutrient pools in the above-ground biomass. Therefore, although redistribution of nutrients within the above-ground biomass was not studied, it is likely that nitrogen, phosphorus and potassium are equally redistributed.

The loss of nitrogen, phosphorus and potassium through flower harvesting represents 59, 54 and 51% of the respective nutrient pools in the above-ground biomass.

3.5.3 Nutrient flows within the plant/soil system

There were three nutrient flows within the system that were studied.

Rainwater fell either directly on to the shrubs or on to the inter-row. The amount of nitrogen in rainwater that fell directly onto the shrubs was 194 mol ha^{-1} yr^{-1}. This is in comparison to the 355 mol ha^{-1} yr^{-1} that fell on to the inter-row and which was unavailable to the *P. neriifolia* shrubs. Of the nitrogen in rainwater that fell directly on to the shrubs, 145 mol ha^{-1} yr^{-1} reached the soil, either as throughfall or stemflow (Figure 3.19a). There was, therefore, a nett gain of 49 mol ha^{-1} yr^{-1} to the nitrogen pool in the above-ground biomass and a nitrogen input into the soil of 145 mol ha^{-1} yr^{-1}. In contrast, the amount of phosphorus in the rainwater that fell on to the inter-row and was unavailable to the *P. neriifolia* shrubs was 8 mol ha^{-1} yr^{-1}

while 4 mol ha^{-1} yr^{-1} fell directly on to the shrubs (Figure 3.19b). However, 10 mol ha^{-1} yr^{-1} reached the soil, either as throughfall or stemflow indicating relatively high levels of phosphorus leaching from the above-ground biomass. There was a nett loss of 6 mol ha^{-1} yr^{-1} of phosphorus from the phosphorus pool in the above-ground biomass and a nett phosphorus input of 10 mol ha^{-1} yr^{-1} into the soil. The movement of potassium follows a similar pattern to that of phosphorus with relatively high leaching of potassium from the above-ground biomass. Potassium in rainwater on to the inter-row was 111 mol ha^{-1} yr^{-1} while 61 mol ha^{-1} yr^{-1} fell directly on to the shrubs (Figure 3.19c). However, 204 mol ha^{-1} yr^{-1} reached the soil, either as throughfall or stemflow indicative of the relatively high levels of potassium leaching mentioned above. There was a nett loss of 143 mol ha^{-1} yr^{-1} of potassium from the potassium pool in the above-ground biomass and a nett potassium input of 204 mol ha^{-1} yr^{-1} into the soil.

The flow of nitrogen (Figure 3.19a), phosphorus (Figure 3.19b) and potassium (Figure 3.19c) through litterfall and decomposition was similar for the three nutrients studied. The rate of nitrogen loss through litter production (376 mol ha^{-1} yr^{-1}) was greater than the rate of potassium loss in litter (17 mol ha^{-1} yr^{-1}) which was greater than the rate of phosphorus loss by litter production (5 mol ha^{-1} yr^{-1}). Similarly, the rate of nitrogen release by litter decomposition (139 mol ha^{-1} yr^{-1}) was greater than that for potassium (3 mol ha^{-1} yr^{-1}) and phosphorus (1 mol ha^{-1} yr^{-1}). As a percentage of nutrients available in the litter, this represents 37% for nitrogen, 26% for phosphorus and 20% for potassium.

Nitrogen was the nutrient acquired in the largest quantities by both above- and below-ground biomass (976 and 99 mol ha^{-1} yr^{-1}) ie. 91% of nitrogen absorbed is translocated to the above-ground biomass and 9% is retained in the below-ground biomass. Potassium was the nutrient taken up in the second largest quantity with 346 mol ha^{-1} yr^{-1} being translocated to the above-ground biomass (96%) and 15 mol ha^{-1} yr^{-1} being retained in the below-ground biomass (4%). The uptake of phosphorus was relatively low compared to that of nitrogen and potassium with 37 mol ha^{-1} yr^{-1} being translocated to the above-ground biomass (95%) and 2 mol ha^{-1} yr^{-1} being retained in the below-ground biomass (5%). For each of the three nutrients, the percentage of nutrients allocated to above- and below-ground biomass was similar.

Nitrogen, phosphorus and potassium pool sizes in the above-ground biomass all showed negative annual increments. This was greater for nitrogen (Figure 3.19a) than for potassium (Figure 3.19c), which was, in turn, greater than for phosphorus (Figure 3.19b). Therefore, for each of the nutrients studied, losses of the nutrients from the above-ground vegetation exceeded inputs. However, despite nutrient deficits the shrubs did continue to grow. In Chapter 5 it will be shown that, for ten year old *P. neriifolia* shrubs that did not receive inorganic fertilizers, this growth occurred at the expense of nutrients already absorbed. Therefore, in these shrubs nutrient concentration declined. This reduction in shrub nutrient status could be predicted using pre- and post-fertilization growth data and pre-fertilization nutrient concentration data.

Similarly, since uptake of the respective nutrients in each case was greater than the inputs from rainwater, throughfall, stemflow and decomposition, it is likely that the growth of the *P. neriifolia* shrubs was at the expense of available nutrients in the soil. This suggests that with time, soil available/soluble nutrient status would decline. This decline was recorded for soluble N, available P and available K in soils that were unamended by inorganic fertilization and this will be discussed in Chapter 5.

Annual increments in the nutrient pools in the below-ground biomass and the litter were positive. Nitrogen increments were greater than for both potassium and phosphorus, respectively.

3.5.4 **Summary**

Figures 3.20a, b and c illustrate annual nutrient budgets for nitrogen, phosphorus and potassium, respectively in summarised form. The plant/soil system (P/SS) is made up of nutrient pools in the above- (AGB) and below- (BGB) ground biomass, available/soluble soil (AS), and total soil (TS). Inputs in this study were from rainwater (R) only, and outputs are due to stream-water (SW) and the loss of nutrients through flower harvesting (FH). Pool units are mol ha^{-1} and flow rate units are mol ha^{-1} yr^{-1}. On a system basis, therefore, there is a nitrogen budget deficit of 691 mol ha^{-1} yr^{-1}, a phosphorus deficit of 28 mol ha^{-1} yr^{-1} and a potassium deficit of 214 mol ha^{-1} yr^{-1}. For nitrogen, the deficit represents 45% of the nitrogen pool in the total biomass; for phosphorus, 50%; and for potassium 41%. This is studied further when considering shrubs that have grown for an additional two years (Chapter 5).

Comparatively, therefore, the deficit in phosphorus is possibly the most limiting to the continued growth of the shrubs although the deficit in each of the nutrients studied will ultimately limit the growth and reproduction of the shrubs.

It is also interesting to note that in the absence of flower harvesting, no deficit for either nitrogen, phosphorus or potassium would occur and there would be an accumulation of each of the nutrients by the plant/soil system. This accumulation would be of the order of 142, 1 and 42 mol ha^{-1} yr^{-1} respectively, and is indicative of efficient internal cycling of nutrients within the plant/soil system (Figures 3.19a, b and c).

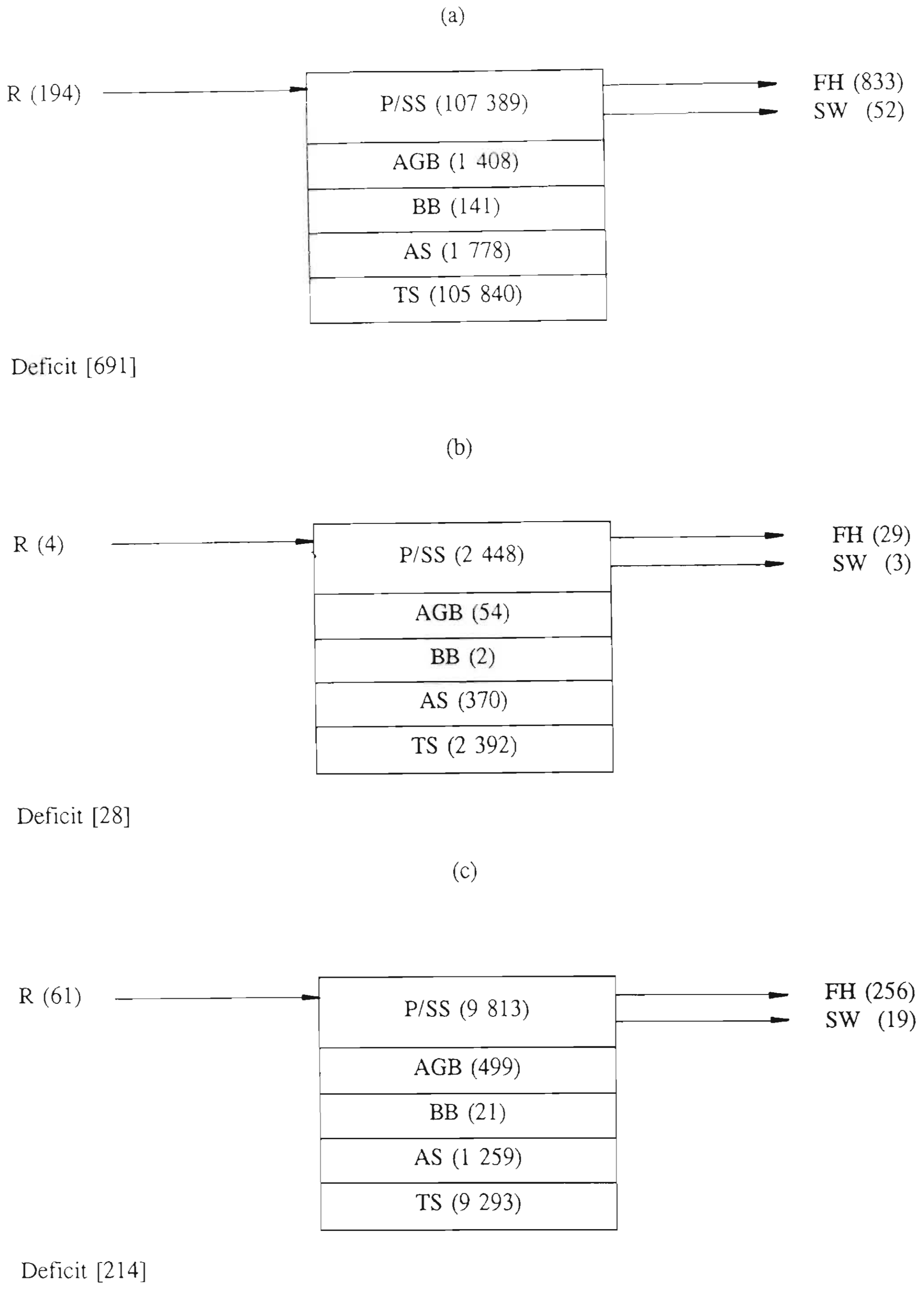


Figure 3.20 Summarised annual nutrient budgets (a) nitrogen, (b) phosphorus, and (c) potassium for *P. neriifolia* cultivated in a summer rainfall area prior to the addition of inorganic fertilizers. The plant/soil system (P/SS) is made up of the nutrient pools in the above- (AGB) and below- (BGB) ground biomass, available/soluble soil (AS), and total soil (TS). Inputs in this study were from rainwater (R) only, and outputs are due to stream-water (SW) and the loss of nutrients through flower harvesting (FH). Pool units are mol ha^{-1} and flux units are mol ha^{-1} yr^{-1}

4 THE EFFECT OF AMMONIUM NITROGEN, PHOSPHORUS AND POTASSIUM ON THE GROWTH OF *PROTEA NERIIFOLIA* SEEDLINGS

The ten control seedlings which received water only died 43 days after transplanting into the standard nursery bags. This suggests there were sufficient seed reserves to last for a maximum of 43 days and, therefore, growth observed over the one year of the experiment was at the expense of applied nutrients.

4.1 Growth responses

The measurements made to determine the effects of applied ammonium nitrogen, phosphorus and potassium on *P. neriifolia* growth were: total stem length, shoot dry mass and root dry mass. Total stem length, shoot dry mass, root dry mass, seedling total dry mass and shoot/root ratio are shown in Tables 4.1, 4.2, 4.3, 4.4 and 4.5, respectively. In each table the data are arranged in order of increasing ammonium nitrogen, increasing phosphorus and increasing potassium levels applied to the seedlings.

Table 4.1 shows increasing total stem length with increasing levels of applied ammonium nitrogen up to the 4 and 7 mM levels. At the highest ammonium nitrogen concentration (10 mM) there was a slight decline in total stem length. Although interactions between applied ammonium, phosphorus and potassium are complex, the influence of phosphorus and potassium is apparent only at moderate levels of applied ammonium nitrogen viz. 4 and 7 mM. At these ammonium nitrogen levels, there is a corresponding increase in total stem length with increasing levels of applied phosphorus and potassium - up to the maximum levels of these two nutrients viz. 0.65 and 1.25 mM, respectively. Similar trends were found for shoot (Table 4.2), root (Table 4.3) and, by calculation, seedling total (Table 4.4) dry mass. In each case, multifactor analysis of variance shows observed interactions to be statistically significant ($P \leq 0.05$). The results of the four multifactor analysis of variance tests are summarised in Table 4.6. Influences of individual nutrients and nutrients in combination are shown by an asterisk (*). Within one nutrient or nutrient

Table 4.1 Seedling total stem length (mm) after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	Potassium concentration (mM)	Nitrogen concentration (mM)			
		1	4	7	10
0.05	0.05	145.78	176.12	172.67	142.22
	0.45	164.34	166.22	145.19	190.21
	0.85	143.89	189.01	195.11	165.44
	1.25	133.89	197.11	141.11	143.11
0.25	0.05	160.33	245.25	173.67	168.11
	0.45	136.67	209.67	192.12	160.11
	0.85	138.33	204.11	254.44	154.75
	1.25	147.33	227.89	164.11	208.78
0.45	0.05	172.89	172.11	268.22	158.89
	0.45	129.89	222.33	226.05	167.33
	0.85	156.67	210.33	216.89	189.56
	1.25	130.22	190.11	197.44	155.67
0.65	0.05	163.33	283.33	244.33	196.13
	0.45	161.67	250.50	221.78	209.89
	0.85	135.56	246.02	226.09	158.33
	1.25	149.78	247.67	245.89	155.33

Table 4.2 Seedling shoot dry mass (g) after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	Potassium concentration (mM)	Nitrogen concentration (mM)			
		1	4	7	10
0.05	0.05	1.33	1.90	1.87	1.33
	0.45	1.47	1.87	1.55	1.76
	0.85	1.06	1.99	2.15	1.55
	1.25	1.28	1.87	1.54	1.04
0.25	0.05	1.12	2.76	1.50	1.61
	0.45	1.38	2.32	2.10	1.65
	0.85	1.09	2.20	2.49	1.75
	1.25	1.29	2.29	1.68	2.12
0.45	0.05	1.44	2.19	3.60	1.74
	0.45	1.22	2.93	3.12	1.44
	0.85	1.58	2.50	2.76	1.69
	1.25	1.35	2.50	2.75	1.62
0.65	0.05	1.46	3.81	3.56	2.05
	0.45	1.47	2.77	2.75	2.09
	0.85	1.75	2.63	3.24	2.36
	1.25	1.85	3.13	3.36	1.62

Table 4.3 Seedling root dry mass (g) after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	Potassium concentration (mM)	Nitrogen concentration (mM)			
		1	4	7	10
0.05	0.05	13.20	18.00	17.81	12.11
	0.45	18.04	27.22	13.21	12.68
	0.85	12.69	24.63	16.93	14.42
	1.25	13.10	25.56	13.23	6.46
0.25	0.05	8.79	22.07	14.40	9.16
	0.45	11.05	21.25	23.13	14.89
	0.85	10.87	27.25	21.03	12.35
	1.25	10.53	30.11	16.37	14.59
0.45	0.05	15.02	26.01	24.79	10.97
	0.45	14.82	25.23	24.59	11.19
	0.85	14.91	20.81	24.62	11.82
	1.25	11.77	25.93	23.16	11.83
0.65	0.05	12.00	24.85	18.06	13.88
	0.45	15.12	20.00	20.04	12.12
	0.85	13.69	19.60	24.99	12.89
	1.25	15.38	22.63	28.14	10.47

Table 4.4 Seedling total dry mass (g) after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	Potassium concentration (mM)	Nitrogen concentration (mM)			
		1	4	7	10
0.05	0.05	14.53	19.90	19.68	13.44
	0.45	19.51	29.09	14.76	14.44
	0.85	13.75	26.62	19.08	15.97
	1.25	14.38	27.43	14.77	7.50
0.25	0.05	9.91	27.83	15.90	10.77
	0.45	12.43	23.57	25.23	16.54
	0.85	11.96	29.45	23.52	14.10
	1.25	11.82	32.40	18.05	16.71
0.45	0.05	16.46	28.29	28.38	12.71
	0.45	16.04	28.16	27.71	12.63
	0.85	16.49	23.31	27.38	13.51
	1.25	13.12	28.43	25.91	13.45
0.65	0.05	13.46	28.66	21.62	15.93
	0.45	16.59	22.77	22.79	14.21
	0.85	15.44	22.23	28.23	15.25
	1.25	17.23	25.76	31.50	12.12

Table 4.5 Seedling shoot/root dry mass ratio after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	**Potassium concentration (mM)**	**Nitrogen concentration (mM)**			
		1	**4**	**7**	**10**
0.05	0.05	0.10	0.11	0.10	0.11
	0.45	0.08	0.07	0.12	0.14
	0.85	0.08	0.08	0.13	0.11
	1.25	0.10	0.07	0.12	0.16
0.25	0.05	0.13	0.13	0.10	0.18
	0.45	0.12	0.11	0.09	0.11
	0.85	0.10	0.08	0.12	0.14
	1.25	0.12	0.08	0.10	0.15
0.45	0.05	0.10	0.08	0.15	0.16
	0.45	0.08	0.12	0.13	0.13
	0.85	0.11	0.12	0.11	0.14
	1.25	0.11	0.10	0.12	0.14
0.65	0.05	0.12	0.15	0.20	0.15
	0.45	0.10	0.14	0.14	0.17
	0.85	0.13	0.13	0.13	0.18
	1.25	0.12	0.14	0.12	0.16

Table 4.6 Summary of the analysis of variance of the interaction and influence of ammonium nitrogen, phosphorus and potassium on the growth of *P. neriifolia* seedlings. For simplicity, analysis of variance results for total stem length, shoot dry mass, root dry mass, seedling total dry mass and shoot/root ratio have been bulked and are presented as one summary. Interactions (*) at the four levels of applied nutrients are indicated.

	Levels			
	1	**2**	**3**	**4**
N	*	**	***	*
P	*	**	**	**
K	*	*	*	*
N and P	*	**	**	*
N and K	*	**	**	*
P and K	*	**	**	**

combination series, significant differences are indicated by different numbers of *'s. For example, for nitrogen influences alone, influences are significantly different between levels 1 and 2, 2 and 3, 3 and 4, and 1 and 3 but not between levels 1 and 4. In contrast, for potassium influences there are no significant differences at the four levels of application.

Shoot/root dry mass ratios (Table 4.5) were extremely low with a mean shoot/root ratio for all the treatments of only 0.12. There was significantly more root than shoot growth with each accounting for a mean 88% and 12% of total growth, respectively. Although low shoot/root ratios are common in seedlings, with predominant root growth affording ecological advantages during the establishment of seedlings (Salisbury and Ross, 1978), shoot/root ratios calculated for *P. neriifolia* seedlings were very low. Shoot/root ratios were low for all levels and combinations of applied ammonium nitrogen, phosphorus and potassium. Ammonium nitrogen did not appear to influence shoot/root ratio. At all levels of applied ammonium nitrogen, moderate to high levels of applied phosphorus (0.25, 0.45 and 0.65 mM) and potassium (0.85 and 1.25 mM) resulted in slightly higher shoot/root ratios, suggesting a greater influence of phosphorus and potassium on above-ground growth. Multifactor analysis of variance showed these interactions between the three applied nutrients on shoot/root ratio to be statistically significant ($P \leq 0.05$) (Table 4.6).

Since the response of seedlings was principally that of a response to applied ammonium nitrogen, with phosphorus and potassium effects only at moderate ammonium nitrogen levels, data has been extracted from Tables 4.1 - 4.5 to illustrate these trends. With increasing levels of applied ammonium nitrogen there is a corresponding increase in total stem length (Figure 4.1), shoot dry mass (Figure 4.2), root dry mass (Figure 4.3) and seedling total dry mass (Figure 4.4) up to applied ammonium nitrogen at 4 and 7 mM. At both low and high levels of applied ammonium nitrogen (1 and 10 mM, respectively), effects of different levels of applied phosphorus and potassium are not apparent and not statistically significant. However, at moderate levels of

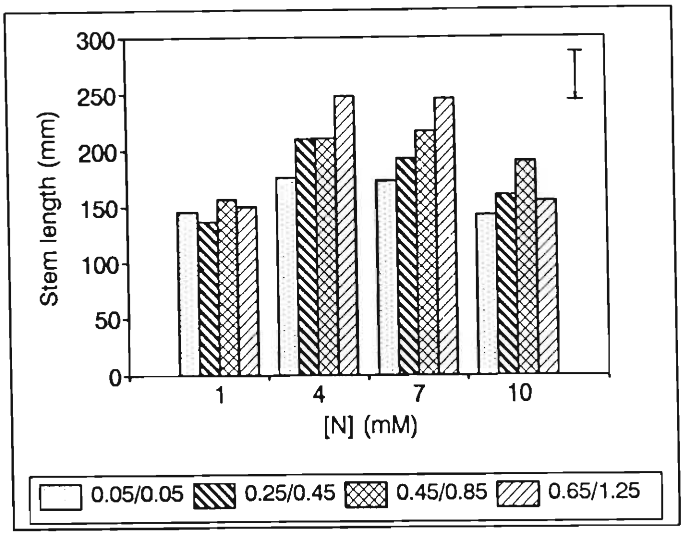


Figure 4.1 Total stem length of seedlings of *P. neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to levels of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference ($P \leq 0.05$).

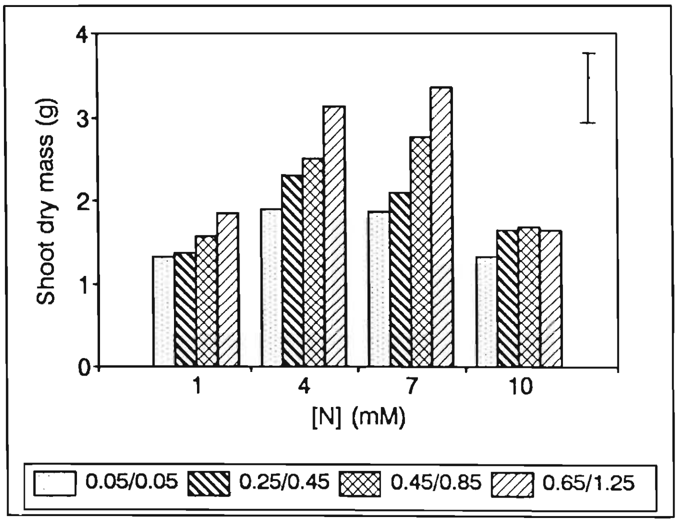


Figure 4.2 Shoot dry mass of seedlings of *P. neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to levels of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference ($P \leq 0.05$).

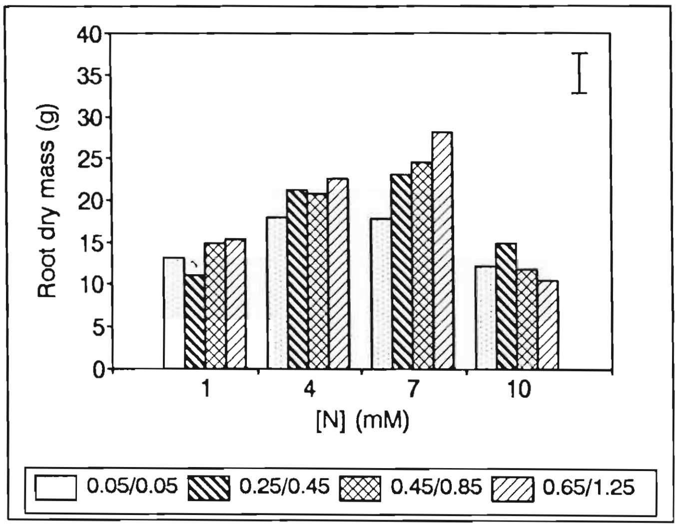


Figure 4.3 Root dry mass of seedlings of *P. neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to levels of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference ($P \leq 0.05$).

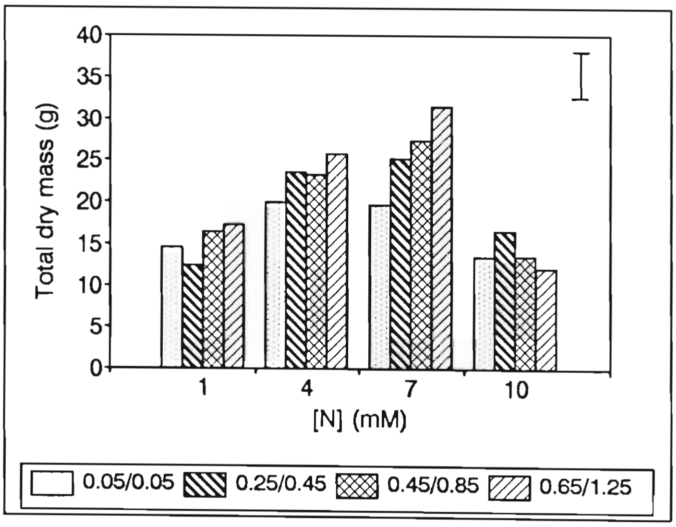


Figure 4.4 Total dry mass of seedlings of *P. neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to levels of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference ($P \leq 0.05$).

applied ammonium nitrogen (4 and 7 mM), with increasing levels of both phosphorus and potassium there is a corresponding increase in each of the plant parameters measured (Figures 4.1 - 4.4). This trend continues to the maximum levels of both phosphorus (0.65 mM) and potassium (1.25 mM) applied to the seedlings, and analysis of variance shows observed differences to be statistically significant.

The greater influence of phosphorus and potassium on shoot growth than on root growth can be seen from Figures 4.2 and 4.3. This is supported by shoot/root dry mass ratios illustrated in Figure 4.5.

4.2 Chemical responses

Seedling nitrogen, phosphorus and potassium concentration after growth for one year under different levels and combinations of applied ammonium nitrogen, phosphorus and potassium are shown in Tables 4.7, 4.8 and 4.9, respectively. Again in each table the data are arranged in order of increasing ammonium nitrogen, increasing phosphorus and increasing potassium levels applied to the seedlings.

With increasing levels of applied ammonium nitrogen there is a corresponding increase in seedling nitrogen concentration (Table 4.7). Different levels and combinations of applied phosphorus and potassium did not appear to affect seedling nitrogen concentration. Seedling phosphorus (Table 4.8) and potassium (Table 4.9) concentrations were varied but relatively constant at all levels of applied ammonium nitrogen, phosphorus and potassium. Multifactor analysis of variance shows these observed trends to be statistically significant ($P \leq 0.05$) (Table 4.10).

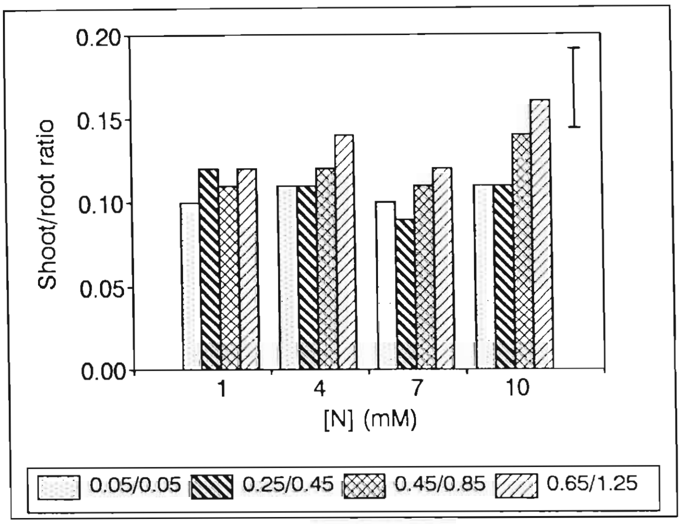


Figure 4.5 Shoot/root dry mass ratio of seedlings of *P. neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to levels of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference ($P \leq 0.05$).

Table 4.7 Seedling nitrogen concentration (mmol g^{-1}) after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	Potassium concentration (mM)	Nitrogen concentration (mM)			
		1	4	7	10
0.05	0.05	0.43	0.53	0.78	0.90
	0.45	0.44	0.65	0.97	1.15
	0.85	0.43	0.59	0.89	1.11
	1.25	0.37	0.55	0.99	1.22
0.25	0.05	0.34	0.49	0.82	1.06
	0.45	0.33	0.55	0.79	0.85
	0.85	0.35	0.57	0.72	0.96
	1.25	0.42	0.57	0.84	0.95
0.45	0.05	0.37	0.49	0.54	1.06
	0.45	0.32	0.52	0.58	0.96
	0.85	0.36	0.48	0.73	0.92
	1.25	0.39	0.55	0.72	1.05
0.65	0.05	0.33	0.43	0.62	0.99
	0.45	0.37	0.47	0.68	0.94
	0.85	0.42	0.45	0.64	1.01
	1.25	0.36	0.47	0.65	1.00

Table 4.8 Seedling phosphorus concentration (mmol g^{-1}) after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	Potassium concentration (mM)	Nitrogen concentration (mM)			
		1	4	7	10
0.05	0.05	0.021	0.018	0.022	0.017
	0.45	0.023	0.021	0.017	0.019
	0.85	0.021	0.017	0.017	0.016
	1.25	0.022	0.018	0.019	0.016
0.25	0.05	0.020	0.019	0.016	0.017
	0.45	0.023	0.023	0.019	0.021
	0.85	0.022	0.021	0.017	0.019
	1.25	0.022	0.018	0.018	0.018
0.45	0.05	0.027	0.021	0.022	0.017
	0.45	0.024	0.020	0.019	0.016
	0.85	0.020	0.021	0.018	0.020
	1.25	0.024	0.022	0.020	0.018
0.65	0.05	0.023	0.022	0.020	0.020
	0.45	0.021	0.023	0.022	0.022
	0.85	0.023	0.021	0.020	0.019
	1.25	0.022	0.023	0.019	0.023

Table 4.9 Seedling potassium concentration (mmol g^{-1}) after growth under various levels and combinations of applied nitrogen, phosphorus and potassium.

Phosphorus concentration (mM)	**Potassium concentration (mM)**	**Nitrogen concentration (mM)**			
		1	**4**	**7**	**10**
0.05	0.05	0.22	0.24	0.24	0.24
	0.45	0.21	0.27	0.23	0.22
	0.85	0.20	0.25	0.22	0.23
	1.25	0.21	0.27	0.22	0.22
0.25	0.05	0.18	0.21	0.25	0.19
	0.45	0.20	0.24	0.26	0.22
	0.85	0.23	0.24	0.24	0.20
	1.25	0.17	0.25	0.25	0.22
0.45	0.05	0.20	0.22	0.27	0.21
	0.45	0.21	0.24	0.24	0.23
	0.85	0.19	0.22	0.25	0.26
	1.25	0.20	0.21	0.26	0.24
0.65	0.05	0.19	0.24	0.25	0.24
	0.45	0.19	0.24	0.26	0.24
	0.85	0.21	0.23	0.27	0.21
	1.25	0.22	0.23	0.24	0.22

Table 4.10 Summary of the analysis of variance of the interaction and influence of ammonium nitrogen, phosphorus and potassium on the nitrogen, phosphorus and potassium concentration of *P. neriifolia* seedlings. Interactions (*) at the four levels of the applied nutrients are indicated.

	Levels			
	1	**2**	**3**	**4**
[N]				
N	*	**	***	****
P	*	**	**	**
K	*	*	*	*
N and P	*	**	***	****
N and K	*	**	**	***
P and K	*	*	*	*
[P]				
N	*	**	**	***
P	*	*	**	**
K	*	*	*	*
N and P	*	**	**	**
N and K	*	*	**	**
P and K	*	*	*	*
[K]				
N	*	**	***	***
P	*	*	*	*
K	*	*	*	*
N and P	*	**	**	*
N and K	*	**	**	*
P and K	*	*	*	*

Influences of individual nutrients and nutrients in combination are shown by an asterisk (*). Within one nutrient or nutrient combination series, significant differences are indicated by different numbers of *'s. For example, for nitrogen influences on seedling nitrogen concentration, influences are significantly different at each level. In contrast, for phosphorus and potassium influences there are no significant differences at the four levels of application.

Increasing seedling nitrogen concentration with increasing levels of applied ammonium nitrogen is clearly illustrated in Figure 4.6. This trend continued to the highest level of applied ammonium nitrogen (10 mM). Since seedlings exhibited reduced growth at the highest level of applied ammonium nitrogen, it is likely that seedling nitrogen content will be lower at this high (10 mM) level of supply than at moderate (4 and 7 mM) levels of supply. This can be illustrated using data extracted from Figure 4.4 (seedling total dry mass) and Figure 4.6 (seedling nitrogen concentration). For example, for [N] = 7 mM, [P] = 0.65 mM and [K] = 1.25 mM, seedling total dry mass is 32 g. For the same NPK combination, seedling nitrogen concentration is 0.63 mmol g^{-1}. Therefore, seedling nitrogen content is 20.16 mmol. In contrast, for [N] = 10 mM, [P] = 0.65 mM and [K] = 1.25 mM, seedling total dry mass is 14 g and seedling nitrogen concentration is 1.0 mmol g^{-1}. Therefore, at this higher level of ammonium nitrogen supply, seedling nitrogen content is 14 mmol ie. lower than seedling nitrogen content of seedlings supplied moderate levels of ammonium nitrogen. Observed increases in seedling nitrogen concentration are, therefore, as a result of the reduced growth of seedlings at higher levels of ammonium nitrogen supply, and not as a result of the absorption of nitrogen in excess of that required for immediate growth ie. luxury consumption.

The variable but relatively constant seedling phosphorus and potassium concentrations are illustrated in Figures 4.7 and 4.8, respectively. Statistical analysis (MSD calculations) shows that at all levels of applied ammonium nitrogen, phosphorus and potassium these observed trends are statistically significant ie. there are differences in seedling phosphorus and potassium

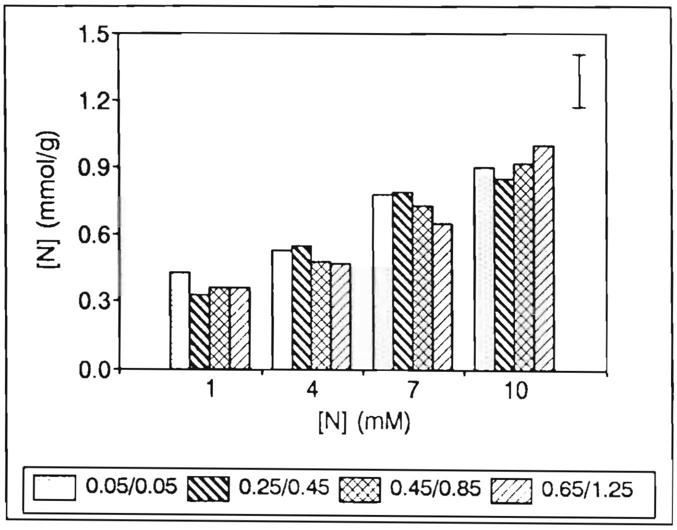


Figure 4.6 Nitrogen concentration of seedlings of *P.neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to the level of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference (P ≤ 0.05).

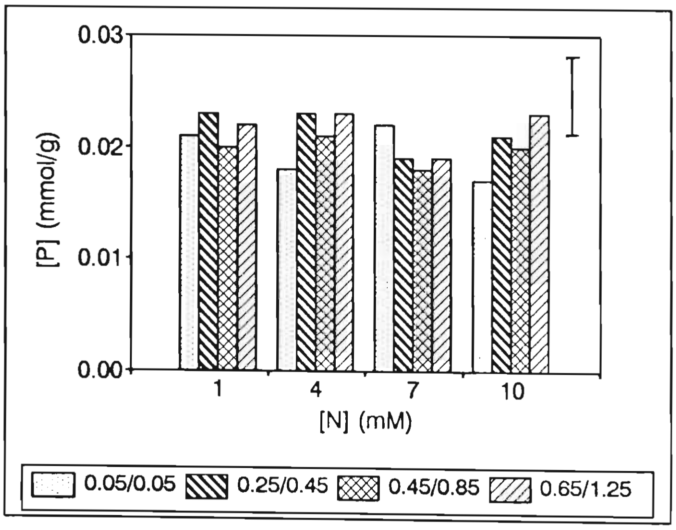


Figure 4.7 Phosphorus concentration of seedlings of *P.neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to the level of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference (P ≤ 0.05).

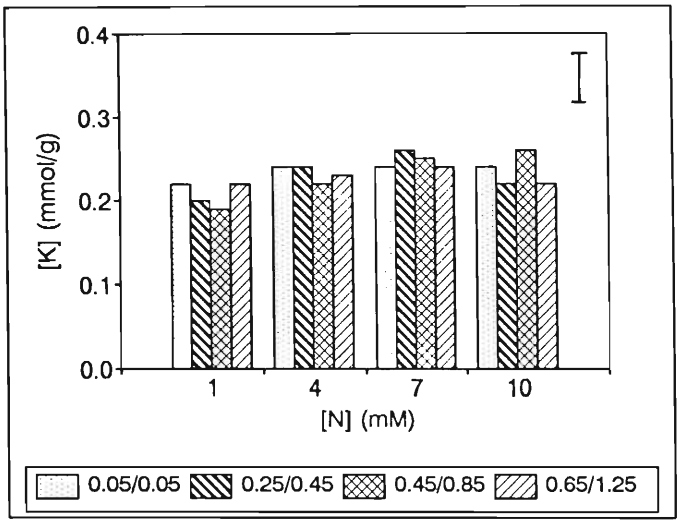


Figure 4.8 Potassium concentration of seedlings of *P.neriifolia* after growth under different nitrogen, phosphorus and potassium regimes. The legends refer to the level of applied phosphorus and potassium (mM). The isolated bar represents the minimum significant difference (P ≤ 0.05).

concentrations but these differences occur within narrow concentration ranges. However, as with seedling nitrogen content, seedling phosphorus and potassium content also varies. At the highest level (10 mM) of ammonium nitrogen supply, growth is less than at moderate (4 and 7 mM) ammonium nitrogen supply. Therefore, since seedling phosphorus and potassium concentrations are similar with all combinations of ammonium nitrogen, phosphorus and potassium, seedling phosphorus and potassium content at high (10 mM) ammonium nitrogen supply is lower than at moderate (4 and 7 mM) levels of applied ammonium nitrogen. Therefore, as in the case of ammonium nitrogen utilization by the seedlings, seedlings absorbed and utilized only as much phosphorus and potassium as required for immediate growth. Therefore, for each of the three nutrients tested there was no evidence of luxury consumption of the nutrients by the seedlings.

4.3 Summary

In summary, therefore, the primary response of seedlings to applied ammonium nitrogen, phosphorus and potassium was increased growth with increasing levels of applied ammonium nitrogen, to a maximum nitrogen level of 7 mM nitrogen. This dominant influence of nitrogen on seedling growth is clearly shown in the analysis of variance tables (Tables 4.6 and 4.10). A secondary response was increased growth with increasing levels of applied phosphorus and potassium, at moderate levels (4 and 7 mM) of applied ammonium nitrogen. Furthermore, there was no evidence to suggest luxury consumption when nutrients were supplied at high levels.

The ammonium nitrogen, phosphorus and potassium regime that resulted in optimum growth of *P. neriifolia* seedlings was N = 7, P = 0.65 and K = 1.25 mM. This converts to an NPK ratio of 10:1:2 (molar basis) or 4.5:1:2.5 (mass basis). This NPK ratio and the requirement that nitrogen should not be in the nitrate form was used as a baseline in the search for a commercially available inorganic fertilizer that best matches *P. neriifolia* requirements. The best match was obtained with Plantosan (Section 2.6) with an NPK ratio of 5:1:3.

Despite the close match of Plantosan to the requirements of *P. neriifolia* seedlings, it was decided to supplement Plantosan with additional nitrogen during field fertilizer trials. This was done for a number of reasons. Firstly, the primary response of seedlings in this experiment was a response to increasing levels of applied ammonium nitrogen. Secondly, during field fertilization it is likely that nitrification of applied ammonium nitrogen will occur. The resultant nitrate nitrogen would be lost to the shrubs, either as a result of leaching through the soil, or as a result of the finding that most Proteaceae have low levels of nitrate reductase and cannot, therefore, efficiently utilize nitrate nitrogen (Stock and Lewis, 1982).

Therefore, to maintain relatively high nitrogen levels, Plantosan was supplemented with either ammonium sulphate or urea. By supplementing with either ammonium sulphate or urea, two forms and two levels of additional nitrogen could be tested to provide baseline data on the most effective fertilizer for the inorganic fertilization of the Proteaceae.

5 THE EFFECT OF INORGANIC FERTILIZER ON GROWTH, PHENOLOGY AND NUTRIENT CYCLING IN AN ESTABLISHED *PROTEA NERIIFOLIA* ORCHARD

Since changes in shrub architecture, growth and nutrient status could be the result of either nutrient additions (inorganic fertilizer applications) or increased age of the shrubs, both nutrient and age related changes were investigated in 9 - 10 year old *P. neriifolia* shrubs. This was possible due to treatment replication during the study of the effects of inorganic fertilizers on the growth, phenology and nutrient cycling in an established *P. neriifolia* orchard. Of the 100 study shrubs, 25 were fertilized with Plantosan plus ammonium sulphate (PAS), 26 with Plantosan plus urea (PU), and 49 shrubs were not fertilized and were used as control (C) shrubs. Nutrient related changes were studied on all 100 shrubs while age related changes were studied on the unfertilized control shrubs.

In the following presentation of results for 9 - 10 year old *P. neriifolia*, certain data have been extracted from Chapter 3 (prefertilization; 7 - 8 year old shrubs) and are presented alongside the current results. Although this does involve limited duplication of prefertilization data, it does provide clarity when discussing nutrient and age related changes in the growth of the *P. neriifolia* shrubs.

5.1 Shrub growth and architecture

Increase in shrub age and the application of inorganic fertilizers both had an effect on a number of *P. neriifolia* shrub dimensions (Table 5.1). Those shrub dimensions which did not show a significant increase in size with increasing shrub age were those that are affected directly by the harvest of flowers, viz. dimensions along and across the line, canopy radius and canopy area. Shrub height, stem diameter and canopy volume all exhibited an expected increase in size with increase in shrub age. This was supported by dry mass increases with increasing shrub age.

Ten year old cultivated *P. neriifolia* shrubs receiving inorganic fertilizers did not show significant differences between fertilizer types but there were

Table 5.1 Shrub dimensions of ten year old *P. neriifolia* cultivated in a summer rainfall area after the addition of inorganic fertilizers: PAS (n = 25), PU (n = 26) and C (n = 49). The dimension data were collected in February 1989. Shrub dry mass for 1988 was determined from an allometric relationship (b) between shrub diameter and shrub dry mass, and shrub dry mass for 1989 is the mean of the actual dry mass of three replicates per fertilizer treatment. Within any one dimension, values followed by different letters are significantly different at $P \leq 0.05$. [Also shown is shrub dimension data (mean ± one standard deviation) for seven year old *P. neriifolia* taken from Table 3.1].

Dimension		**PAS**	**PU**	**C**	**Seven year old** ***P. neriifolia***
Height	m	3.12^{a}	2.92^{a}	2.57^{b}	1.97 ± 0.27
Stem diameter	cm	9.74^{a}	9.46^{a}	8.85^{b}	7.21 ± 1.62
Dimension along line	m	1.73^{a}	1.92^{a}	1.89^{a}	1.78 ± 0.48
Dimension across line	m	2.56^{a}	2.54^{a}	2.46^{a}	2.44 ± 0.45
Canopy radius	m	1.07^{a}	1.12^{a}	1.09^{a}	1.06 ± 0.19
Canopy area	m^2	3.60^{a}	3.94^{a}	3.73^{a}	3.53 ± 0.63
Canopy volume	m^2	11.23^{a}	11.51^{a}	9.59^{b}	6.95 ± 2.07
Shrub dry mass - 1988	kg	8.70^{a}	5.45^{a}	7.87^{a}	3.83 ± 0.41[1]
Shrub dry mass - 1989	kg	16.81^{a}	14.61^{a}	11.18^{b}	6.48 ± 0.72[2]

[1] dry mass 1986

[2] dry mass 1987

significant differences between fertilized and unfertilized shrubs. These differences were most apparent for shrub height and stem diameter. Shrub dimensions along and across the line and canopy radius are affected by the harvesting of flowers and consequently did not show significant differences between the fertilized and unfertilized shrubs. Canopy area is derived from the canopy radius and, therefore, did not show differences between the shrubs. However, shrub volume which incorporates the height of the shrubs did show a significant difference between fertilized and unfertilized shrubs.

Shrub dry mass data for 1988 and 1989 are also presented in Table 5.1. The dry mass data for 1988 are derived from an allometric relationship (b) between stem diameter and shrub dry mass (Section 2.2.1.1), while 1989 data were obtained from actual shrubs removed, dried and weighed. For 1988 there is no significant difference in shrub dry mass between fertilized and unfertilized plants. However, the actual dry masses measured in 1989 do show significant differences. There is no difference between the two fertilizer treatments but there is a difference between those shrubs that received inorganic fertilizers and those shrubs that were not fertilized. Given the lack of differences between shrubs in 1988, it is possible that the allometric relationship resulted in an underestimate of shrub dry mass, or alternatively, the effects of fertilizers became apparent only at a later stage, at least one year after the initial application.

Figure 5.1 illustrates the respective contributions of the shrub components to shrub dry mass and although there are differences between fertilized and unfertilized shrubs, in each case the contribution of stems to total dry mass accounts for over half the dry mass of the shrubs. This was the case with shrubs prior to the application of inorganic fertilizers (66%) (Figure 3.1), and since in the case of fertilized shrubs the percentage contribution is of the same order, there appears to be no change in allocation to stem dry matter with age. However, with unfertilized shrubs the percentage contribution of stems to total dry mass was slightly reduced (57%) suggesting a possible change in dry matter allocation patterns.

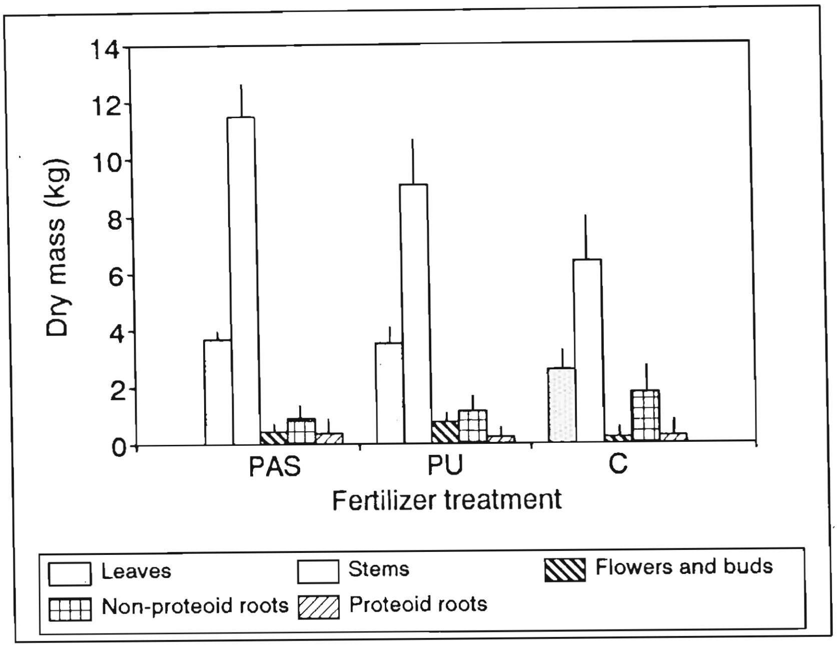


Figure 5.1 Dry mass of shrub components of ten year old *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). Values are the mean (± one standard deviation) of three shrubs per fertilizer treatment.

Considering the other shrub components, there does appear to be a change in allocation patterns in non-proteoid roots (Table 5.2). In seven year old *P. neriifolia*, non-proteoid roots accounted for 8% of the total dry matter. In ten year old *P. neriifolia* fertilized with PAS, there has been a decline to 5%. In those shrubs fertilized with PU the percentage contribution of non-proteoid roots to total dry mass is of the same order as in seven year old shrubs (8%). However, in unfertilized ten year old shrubs, non-proteoid roots account for 16% of the total dry mass. Although there was not a corresponding increase in proteoid roots, this increased dry matter allocation to non-proteoid roots in unfertilized shrubs could be indicative of nutrient-limited soils. Furthermore, it appears that this increase in dry matter allocation to non-proteoid roots occurred at the expense of stem material (Table 5.2). This suggests that soil nutrients and age both influence the shoot/root ratio.

There also appears to be a change in dry matter allocation to the flowers and buds (Table 5.2). Since this allocation in seven and fertilized ten year old *P. neriifolia* shrubs is similar, with a reduction in unfertilized ten year old shrubs, it would appear that this change in dry matter allocation patterns is nutrient related.

All other allocation patterns in PAS, PU and C shrubs are similar to allocation patterns in seven year old shrubs prior to the application of inorganic fertilizers (Table 5.2).

Since there are differences in dry matter allocation patterns with age and with the application of inorganic fertilizers it can be expected that there will be differences in shoot/root and leaf/stem dry mass ratios (Table 5.3). There has been an increase in shoot/root dry mass ratio from 8.8 kg kg^{-1} (seven year old *P. neriifolia*) to 12.6 and 10.1 kg kg^{-1} for shrubs fertilized with PAS and PU, respectively ie. there was an increase in allocation of dry matter to shoots relative to roots. In contrast, the shoot/root dry mass ratio has decreased for unfertilized shrubs indicative of the greater dry mass allocation to the roots in

Table 5.2 Comparison of dry matter allocation (%) in ten year old *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes. Also shown are allocation data for seven year old *P. neriifolia*.

	PAS	**PU**	**C**	**Seven year old *P. neriifolia***
Leaves	22	24	23	20
Stems	68	62	57	66
Flowers and buds	3	5	2	4
Non-proteoid roots	5	8	16	8
Proteoid roots	2	1	2	2

Table 5.3 Shoot/root dry mass ratio and leaf/stem dry mass ratio of *P. neriifolia* cultivated in a summer rainfall area with and without the application of inorganic fertilizers. [Data for seven year old shrubs are also presented (Section 3.1).]

	Shoot/root ratio (kg kg^{-1})	**Leaf/stem ratio (kg kg^{-1})**
PAS	12.6^a	0.317^a
PU	10.1^a	0.387^b
C	4.5^b	0.400^b
7 year old	8.8^c	0.303^a

Within any one parameter, values followed by different letters are significantly different ($P \leq 0.05$).

these shrubs. The differences in shoot/root dry mass ratio as a result of the application of inorganic fertilizers are significant between fertilized and unfertilized shrubs but are not significant between the two fertilizer treatments. Differences in shoot/root dry mass ratio between seven year old and fertilized and unfertilized ten year old *P. neriifol*ia shrubs are also statistically significant (Table 5.3).

Shrubs fertilized with PAS showed no change in leaf/stem dry mass ratio with age (0.303 to 0.317 kg kg^{-1}) (Section 3.1 and Table 5.3). However, shrubs fertilized with PU and unfertilized control shrubs showed an increase, from 0.303 to 0.387 and 0.4 kg kg^{-1}, respectively (Section 3.1 and Table 5.3). Since these differences in leaf/stem dry mass ratio between fertilizer treatments and between fertilized and unfertilized control shrubs are statistically significant, this increase reflects a change in dry matter allocation patterns between leaves and stems with more dry matter being allocated to leaf material.

Maximum leaf area per stem cross-sectional area was recorded in late spring/summer (November to February) with reduced leaf areas in winter (June and July) (Figure 5.2). Since this is in accordance with seasonal variations in leaf area described in Section 3.1, patterns of seasonality of *P. neriifolia* leaf area per stem cross-sectional area did not change with age or with the application of inorganic fertilizers (Figure 5.2). This is reflected by similar mean leaf area per stem cross-sectional area for seven and ten year old *P. neriifolia*, with or without the application of inorganic fertilizers (Table 5.4). Similarly, there is no change in leaf area ratio with age or with the application of inorganic fertilizers. However, there are significant differences in leaf area index, both with age and as a result of the application of inorganic fertilizers. All shrubs, irrespective of the fertilizer treatment showed significantly greater leaf area index with age. Furthermore, fertilized shrubs had a leaf area index significantly greater than unfertilized shrubs. However, differences between the two fertilizer types were not significant. This increase in leaf area index with age and with inorganic fertilization suggests an

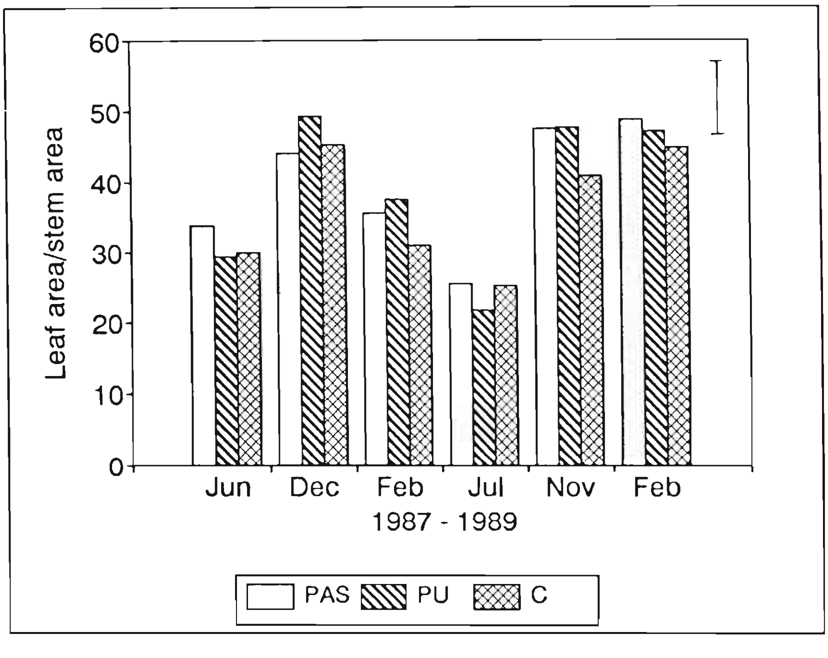


Figure 5.2 Seasonal variations in leaf area per stem cross-sectional area ($mm^2 mm^{-2}$) of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

Table 5.4 Mean leaf area per stem cross-sectional area, leaf area ratio, and leaf area index of *P. neriifolia* cultivated in a summer rain-fall area with and without the application of inorganic fertilizers. [Also shown are comparative data for seven year old *P. neriifolia* taken from Table 3.2.]

	Leaf area (mm^2 mm^{-2})	**Leaf area ratio (m^2 kg^{-1})**	**Leaf area index (m^2 m^{-2})**
PAS	39.62^a	1.036^a	4.643^a
PU	39.59^a	1.146^a	4.206^a
C	36.88^a	1.092^a	3.180^b
7 year old	37.17^a	0.954^a	1.009^c

Within any one parameter, values followed by different letters are significantly different ($P \leq 0.05$).

increased leaf cover of the ground area above which the shrub canopy has grown ie. the shrub canopy has become more dense with available space being occupied by leaves. It is important to note that leaf area index refers to the individual shrubs and not to the whole plant community. Nevertheless, considering that leaves are relatively long-lived (Figure 3.3), with continued leaf production and a relatively constant canopy area (Table 5.1), leaf area index will increase. Leaf area ratio remained low because of stem production to carry the leaves.

Figure 5.3 illustrates the longevity of leaves of *P. neriifolia* cultivated in a summer rainfall area with and without the application of inorganic fertilizers. Inorganic fertilizers did not affect the longevity of leaves. This apparent lack of influence of inorganic fertilizers on leaf longevity was possibly as a result of fertilizers being applied only 10 months after the start of the trial. Thirty two months after leaves were tagged, shrubs receiving PAS retained 45% of the leaves originally tagged, shrubs receiving PU, 40%, and shrubs receiving no inorganic fertilizers, 40%. This relatively long lifespan of *P. neriifolia* leaves supports the increasing leaf area index recorded for the shrubs (Table 5.4).

Changes in leaf nitrogen, phosphorus and potassium levels with leaf age are illustrated in Figures 5.4a, b and c, respectively. For the three nutrients, irrespective of fertilizer treatment, leaf nutrient level changes with age followed the same pattern and were of the same order. As with leaf longevity, this apparent lack of influence of inorganic fertilizers on leaf nutrient levels with age was probably a result of fertilizers being applied only 10 months after the start of the trial. As will be shown later (Section 5.4.1), there was considerable variation in leaf nutrient concentration, both between unfertilized and fertilized shrubs, and between fertilizer treatments. Leaf nitrogen levels (Figure 5.4a) were greatest in the youngest leaves. The greatest drop in leaf nitrogen levels occurred in the first three months after leaf production. Thereafter, leaf nitrogen levels continued to decrease at a slower and relatively constant rate. Similarly, leaf phosphorus levels (Figure 5.4b) were

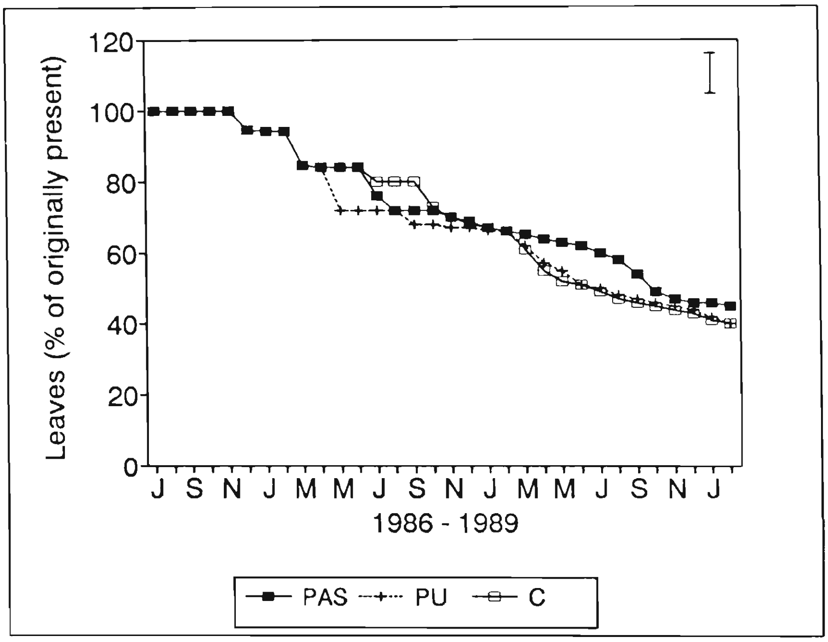


Figure 5.3 Leaf longevity, measured as a percentage of the total leaves tagged, of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). In each case the isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

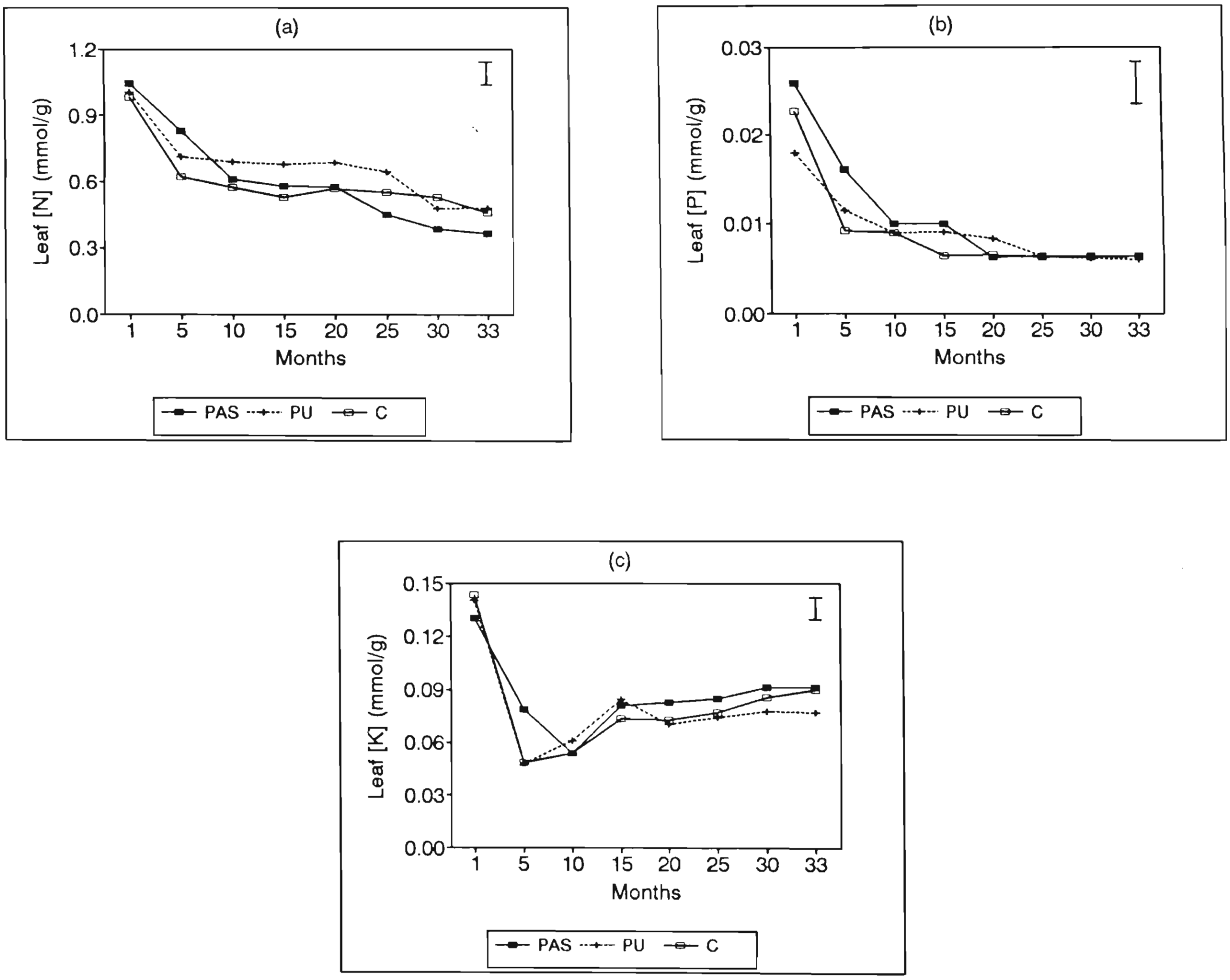


Figure 5.4 Variations in leaf (a) nitrogen, (b) phosphorus, and (c) potassium concentration with increasing leaf age of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). In each case the isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

greatest in the youngest leaves with the sharpest drop in leaf phosphorus levels occurring in the first eight months after leaf production. Thereafter, leaf phosphorus levels remained relatively constant for the balance of the study period of 32 months. Therefore, nitrogen and phosphorus levels are greatest in the newly produced leaves, with export of nitrogen and phosphorus to other shrub parts, including further new leaves, occurring within the first three and eight months, respectively. Fluctuations in leaf potassium levels (Figure 5.4c) were quite dissimilar to those of nitrogen and phosphorus. Leaf potassium levels were greatest in the youngest leaves with a sharp drop within the first four months. Following this initial decline leaf potassium levels were relatively constant for six months. Thereafter leaf potassium levels started to increase to a level approximately half that of newly produced leaves. This occurred in leaves of shrubs either receiving or not receiving inorganic fertilizers and there were no significant differences in leaf potassium levels between the different fertilizer treatments. It appears, therefore, that leaves accumulate potassium with age, suggesting sufficient or excess potassium is available for shrub growth, in the presence or absence of inorganic fertilizers. There is no comparative data on leaf nutrient level changes with age for younger *P. neriifolia* shrubs.

Flower head (florets and bracts) dry mass varied seasonally with larger flowers being produced early in the flowering season (February and March) (summer/early autumn) and smaller flowers being produced during the balance of the year (Figure 5.5). Initially the application of inorganic fertilizers to shrubs did not have a significant affect on flower size. However, 22 to 26 months after the initial fertilizer applications, significant increases in flower size for shrubs fertilized with Plantosan plus ammonium sulphate and Plantosan plus urea were evident. There were, however, no significant differences in flower size between the inorganic fertilizer treatments.

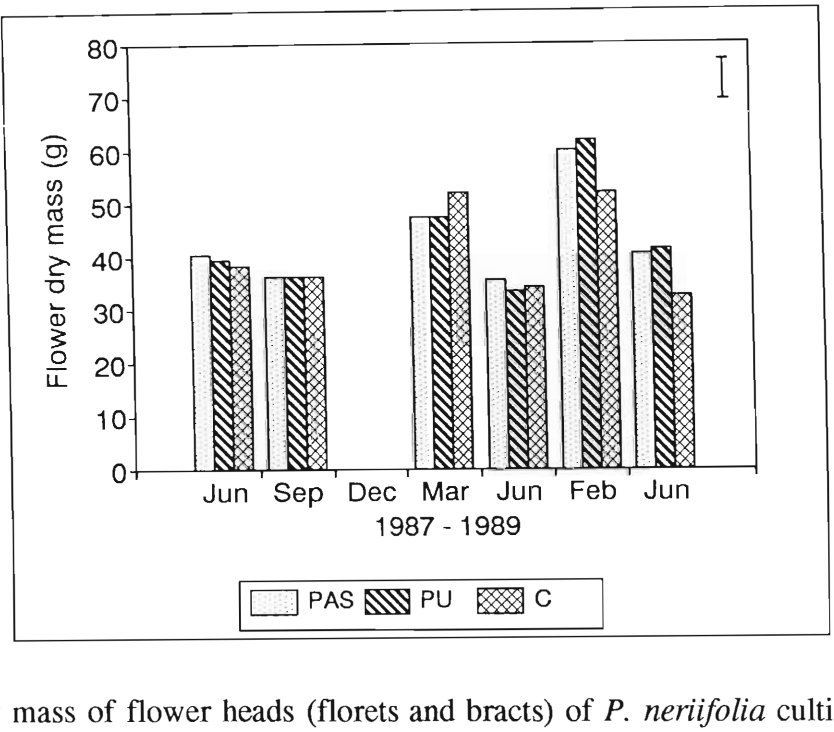


Figure 5.5 Dry mass of flower heads (florets and bracts) of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

5.2 Shrub phenology

5.2.1 Shoot growth and flowering

Shoot growth (20 months) and flower production (24 months) of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes are summarised in Table 5.5. There were a number of significant differences between the fertilizer treatments. Of the primary shoots originally tagged for measurement, shrubs receiving PU produced more reproductive primary shoots (80%) than shrubs receiving PAS (60%) or control shrubs (40%). However, shrubs receiving PAS produced more reproductive lateral shoots (30%) than shrubs receiving PU (20%) or control shrubs (15%). Shrubs from each of the three fertilizer treatments produced similar numbers of lateral shoots from primary shoots and lateral shoots from lateral shoots. However, there were significant differences in total shoot growth (ie. the sum of primary, lateral and secondary lateral shoot growth) between fertilized (666 and 709 mm for PAS and PU shrubs, respectively) and unfertilized (552 mm) shrubs. Similarly, there were significant differences in shrub flower production and associated dry mass loss between fertilized (135 and 139 flowers, and 8.9 and 9.8 kg for PAS and PU shrubs) and unfertilized (94 flowers, and 6.2 kg) shrubs, respectively. For total shoot growth, and flower production and associated dry mass loss, differences between fertilizer treatments were not significant.

Comparisons with shrub annual growth prior to the application of inorganic fertilizers ie. 1984/1985, 1985/1986 and 1986/1987 (Table 3.3) are not entirely valid as shoot growth data presented in Table 5.5 are for 20 months and flower production data are for 24 months (Table 5.5). Comparative mean growth per month data are presented in Table 5.6. There are no significant differences in numbers of lateral shoots produced from primary shoots with increasing age of the shrubs or due

Table 5.5 Comparison of phenological characteristics and growth data of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (C), and unfertilized control shrubs (C). Data presented are for 20 months (shoot growth) and 24 months (flower production).

	PAS	**PU**	**C**
% primary shoots remaining vegetative	40^{a}	20^{b}	60^{c}
% primary shoots becoming reproductive	60^{a}	80^{b}	40^{c}
% primary shoots dead	0^{a}	0^{a}	0^{a}
Mean no of lateral shoots per primary shoot	2.40^{a}	2.30^{a}	2.20^{a}
Mean no of lateral shoots per lateral shoot	0.08^{a}	0.07^{a}	0.08^{a}
% lateral shoots remaining vegetative	65^{a}	75^{a}	85^{b}
% lateral shoots becoming reproductive	30^{a}	20^{a}	15^{b}
% lateral shoots dead	5^{a}	5^{a}	0^{a}
Total growth (primary and all lateral shoots) per primary shoot (Jul 87 - Feb 89) (mm)	666^{a}	709^{a}	552^{b}
Mean no of flowers per shrub (Jul 87 - Jun 89)	135^{a}	139^{a}	94^{b}
Mean dry mass loss per shrub (Jul 87 - Jun 89)*	8.9^{a}	9.8^{a}	6.2^{b}

* dry mass loss as a result of the harvesting of flowers.

Within any one parameter, values followed by different letters are significantly different ($P \leq 0.05$).

Table 5.6 Comparative shoot growth and flower production data for *P. neriifolia* cultivated in a summer rainfall area prior to the application of inorganic fertilizers (PF) and after growth under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). Data are presented as mean growth per month. Prefertilization data from Table 3.3 excludes the 1986-1987 period because of the influence of hail in this period. Postfertilization data are from Table 5.5.

	PF	**PAS**	**PU**	**C**
Mean no of lateral shoots/primary shoot/month	0.14^a	0.12^a	0.12^a	0.11^a
Mean monthly growth of all shoots (mm)	36.88^a	33.30^a	35.50^a	27.60^b
Mean monthly flower production/shrub	2.33^a	5.63^b	5.79^b	3.92^c
Mean monthly dry mass loss/shrub* (kg)	0.11^a	0.37^b	0.41^b	0.26^c

* dry mass loss as a result of the harvesting of flowers.

Within any one parameter, values followed by different letters are significantly different ($P \leq 0.05$).

to inorganic fertilizer applications. There are, however, significant differences in the mean monthly growth of all shoots: between shrubs prior to fertilization and unfertilized control shrubs, and between fertilized and unfertilized shrubs. There are no significant differences in the mean monthly growth of all shoots between shrubs prior to fertilization and fertilized shrubs (PAS and PU treatments). In summary, therefore, there is a reduction in mean monthly shoot growth with age in unfertilized shrubs, while this reduction in growth is reversed by the application of inorganic fertilizers. There are also significant differences in the mean monthly flower production per shrub. There is an increase in flower production with age and as a result of the application of inorganic fertilizers. These differences are also applicable to dry mass loss as a result of the harvesting of flowers.

The timing of shoot growth and flowering did not change with age or due to the application of inorganic fertilizers and was the same as described in Section 3.2.1, Figures 3.4, 3.5 and 3.6, and Table 3.4. For conciseness, therefore, the data for the 1987/1989 period are not presented. Rather, in summary, peak vegetative growth (primary and all lateral shoots) occurred in September (early spring) with summer (December, January and February) growth rates being only slightly higher than in autumn (March, April and May) or winter (June, July and August). Flowering occurred from January to July with the maximum yield of commercially harvestable flowers in March, April and May (autumn) when active vegetative growth is lowest.

Periodicity in occurrence and quantification of proteoid and non-proteoid roots were not studied during the 1987-1989 period.

5.3 Litter production

For each fertilizer treatment, peak litter production was recorded during August, September and October (late winter/spring) with distinctly lower levels of litter loss for the period November to July (late spring/summer/winter) (Figure 5.6). This seasonal variation in litter production is similar to that described in Section 3.3.1 and illustrated in Figure 3.9 suggesting no change in seasonality with increasing shrub age. Similarly, statistical analysis shows that different fertilizers did not significantly affect either the seasonal nature of litter production or the quantity of litter production per annum (Figure 5.6). Increasing shrub age and fertilizer applications did not affect the composition of litter, with leaf litter continuing to contribute over 90% of the total litter in each month.

The loss of nitrogen (Figure 5.7a), phosphorus (Figure 5.7b) and potassium (Figure 5.7c) all exhibited distinct seasonal variation with peak loss occurring between August and October (late winter/spring) and little variation in loss for the period November to July (late spring/summer/winter). This seasonal variation followed the same pattern as total litter production (Figure 5.6) and was also similar to nutrient loss from *P. neriifolia* shrubs prior to the application of inorganic fertilizers (Figure 3.10a, b and c). There is, therefore, no change in nutrient loss with increasing age of the shrubs. Similarly, statistical analysis shows there are no differences in nutrient loss between fertilized and unfertilized shrubs or between shrubs receiving different fertilizer types. Of interest, in Section 3.3.1 it was noted that nitrogen concentration of the litter showed seasonal variation during the year. The close match between total litter loss and nitrogen loss curves for the 1988-1989 period shows no variation in nitrogen concentration of litter in these older shrubs.

Litter decomposition rates were not studied during the 1987-1989 period and decomposition values recorded for the prefertilization period (Section 3.3.2) will be used for nutrient budgets in the postfertilization period (Section 5.5).

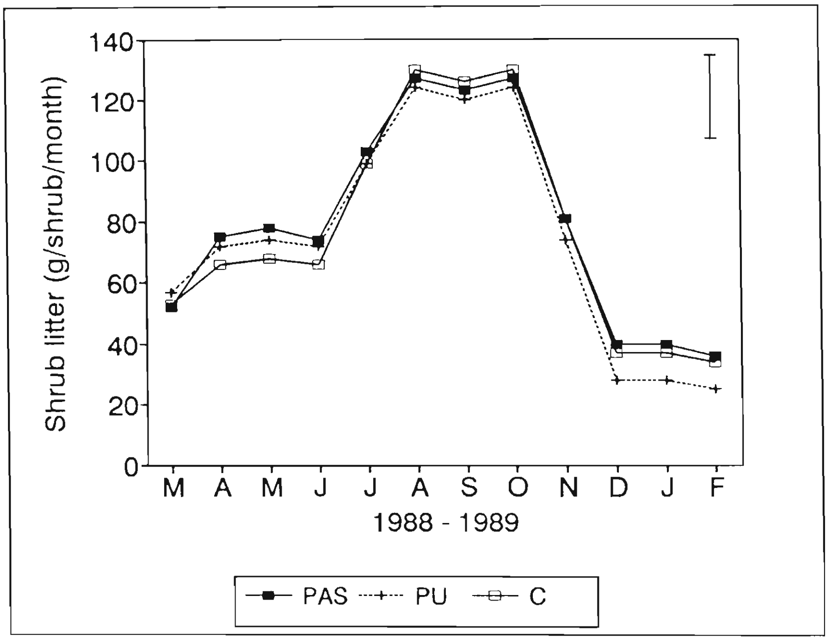


Figure 5.6 Seasonal variation in total litter production from *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

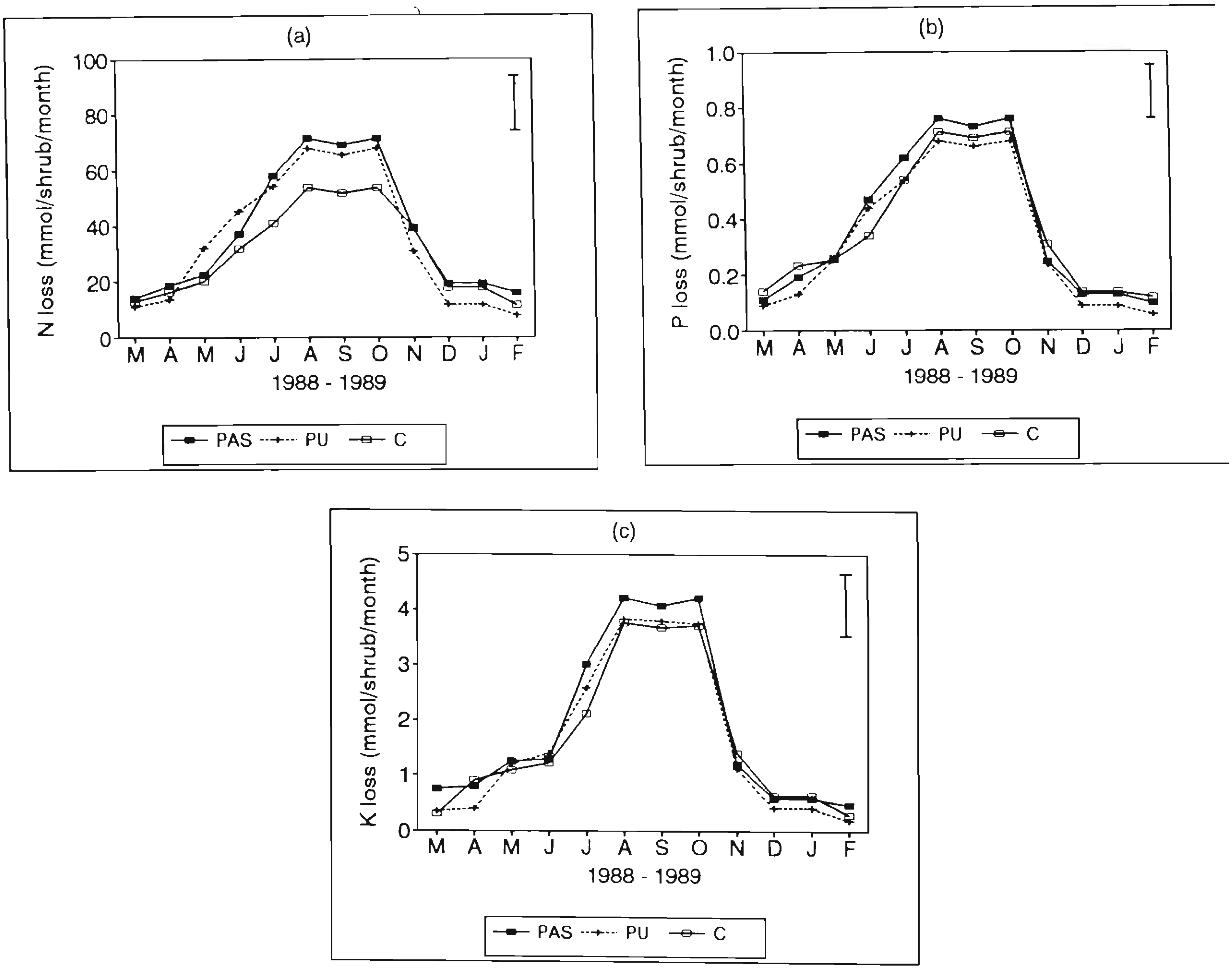


Figure 5.7 Seasonal variation in total (a) nitrogen, (b) phosphorus, and (c) potassium loss during litter production from *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

5.4 Nutrient status

5.4.1 Shrub nutrient status

The concentration of nitrogen in leaves and stems of shrubs grown under PAS (Figure 5.8a), PU (Figure 5.8b) and without inorganic fertilizers (Figure 5.8c) showed little seasonal variation with or without the application of inorganic fertilizers. This is in contrast to nitrogen concentrations in leaves and stems prior to inorganic fertilization when nitrogen levels were greatest in late winter/spring and lowest in late spring/summer (Figure 3.15a). However, the levels of nitrogen in these shrub parts did vary with treatment, with levels in shrubs fertilized with PAS being double the nitrogen levels in both shrubs fertilized with PU and in unfertilized shrubs. Since leaf and stem nitrogen levels in shrubs fertilized with PAS are comparable to levels prior to the application of inorganic fertilizers (Figure 3.15a), there is a reduction in nitrogen levels in leaves and stems of shrubs fertilized with PU (Figure 5.8b) and unfertilized shrubs (Figure 5.8c).

Floret and bract nitrogen concentrations (Figures 5.9a, b and c) showed a peak between July and November (winter/spring) with reduced levels in February and March (late summer/early autumn), irrespective of the fertilizer treatment. This seasonal trend is similar to that found in florets and bracts prior to the application of inorganic fertilizers (Figure 3.15b), and statistical analysis shows differences to be significant. The concentration of florets and bracts from shrubs fertilized with PAS and PU are of the same order and are similar to levels prior to fertilization (Figure 3.15b). In contrast, however, nitrogen levels of florets and bracts of unfertilized shrubs are lower than those in fertilized shrubs and lower than those in shrubs prior to the application of inorganic fertilizers.

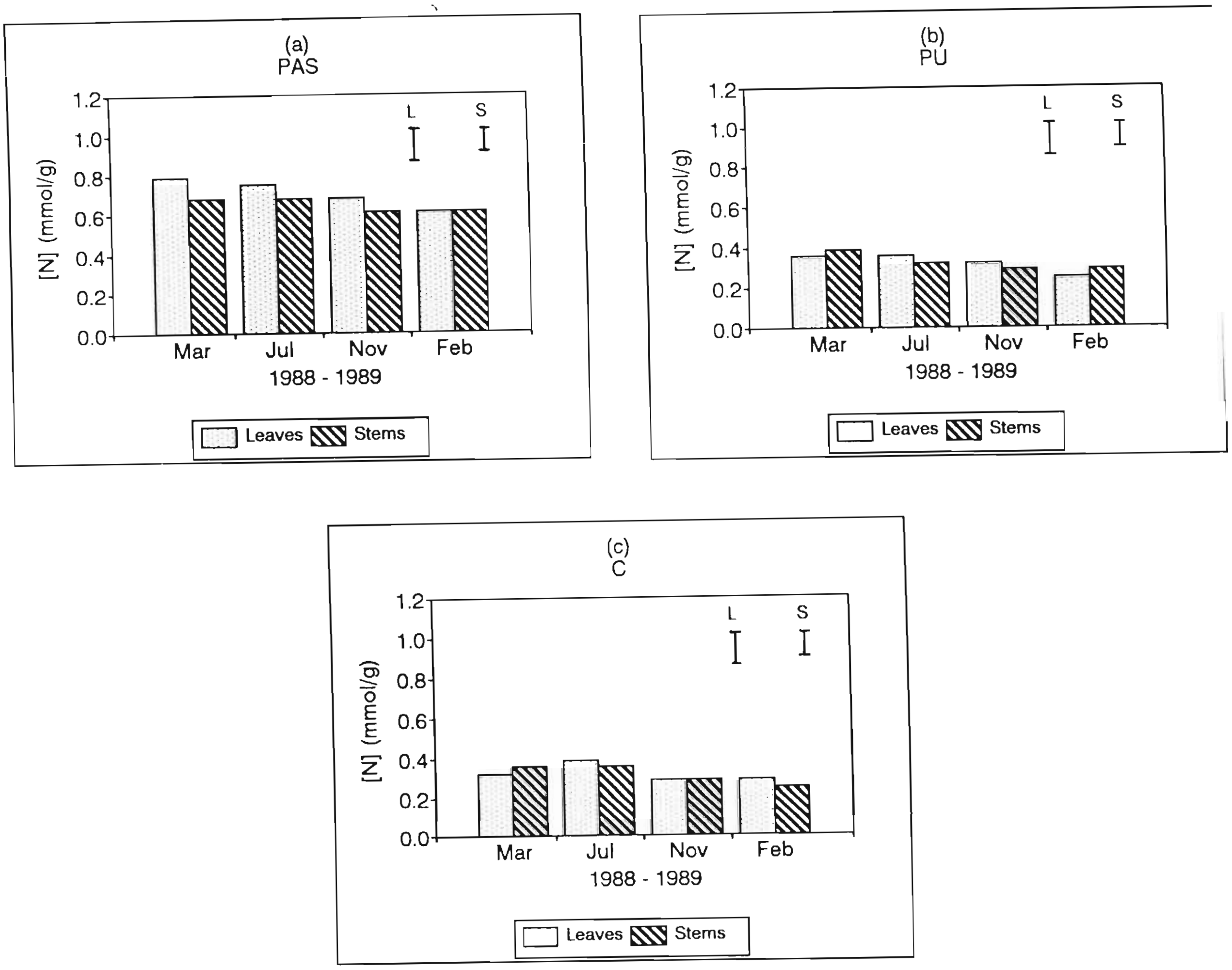


Figure 5.8 Seasonal variation in nitrogen concentration in leaves and stems of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: (a) Plantosan plus ammonium sulphate (PAS), (b) Plantosan plus urea (PU), and (c) unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

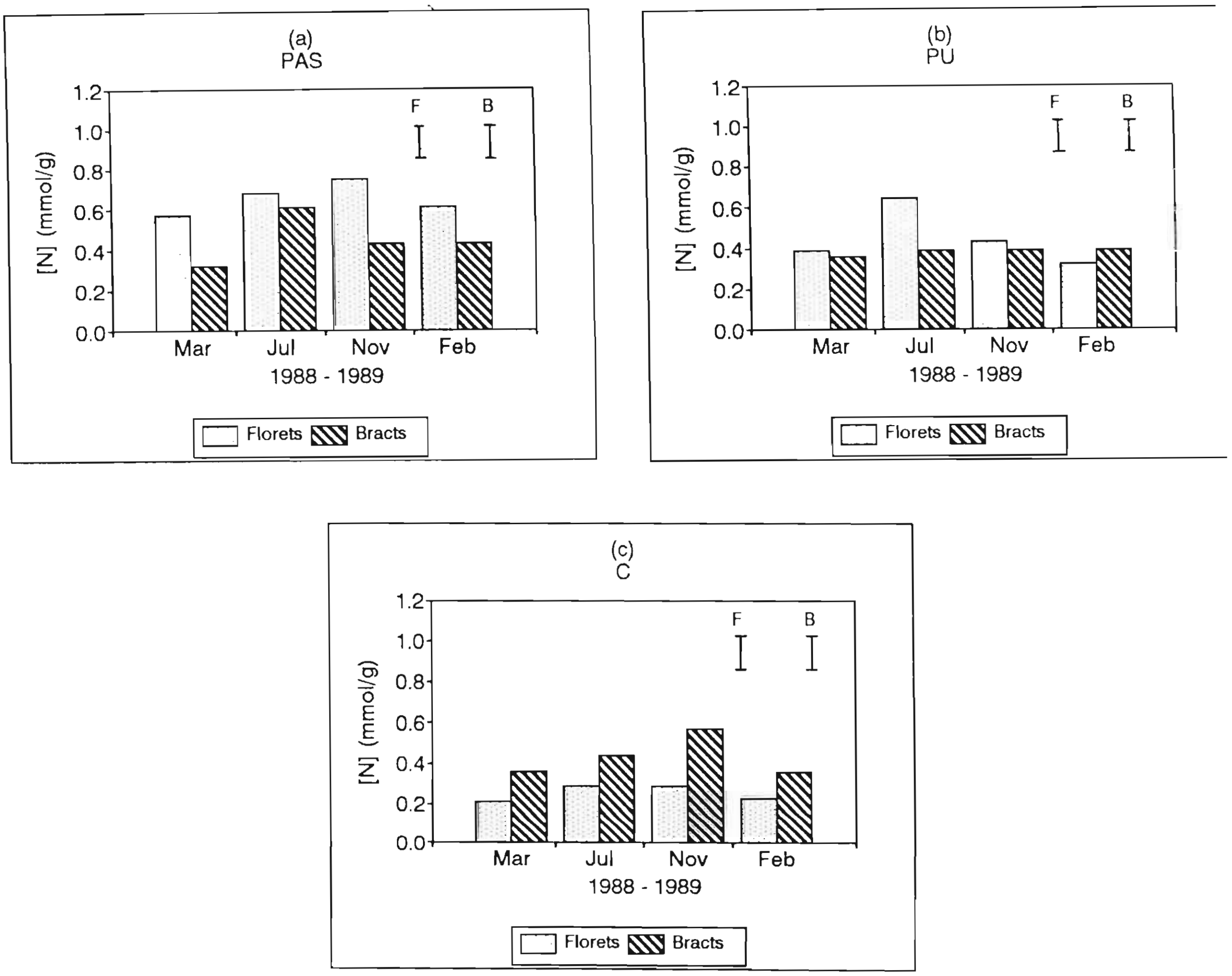


Figure 5.9 Seasonal variation in nitrogen concentration in florets and bracts of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: (a) Plantosan plus ammonium sulphate (PAS), (b) Plantosan plus urea (PU), and (c) unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

In shrubs fertilized with PAS (Figure 5.10a), leaf and stem phosphorus concentrations were greatest between March and July (autumn/winter) and lowest between November and February (late spring/summer). In shrubs fertilized with PU (Figure 5.10b) and in unfertilized shrubs (Figure 5.10c) this seasonality was not significant. For shrubs fertilized with PAS, both leaf and stem phosphorus levels and the seasonal pattern in leaf and stem phosphorus concentration were similar to that of shrubs prior to the application of inorganic fertilizers (Figure 3.16a). In shrubs fertilized with PU (Figure 5.10b) and unfertilized shrubs (Figure 5.10c), however, leaf and stem phosphorus levels were lower than for shrubs fertilized with PAS (Figure 5.10a) and shrubs prior to the application of inorganic fertilizers (Figure 3.16a). Statistical analysis shows these differences to be significant ($P \leq 0.05$).

Shrubs from each of the three fertilizer treatments showed seasonal trends in floret and bract phosphorus concentrations with greatest concentration between July and November (winter/spring) and lowest concentration between February and March (late summer/autumn) (Figures 5.11a, b and c). These trends are similar to those found in shrubs prior to the application of inorganic fertilizers (Figure 3.16b). Statistical analysis shows these trends are significant for shrubs fertilized with PAS but not for shrubs fertilized with PU and unfertilized shrubs. Similarly, statistical analysis shows that levels of phosphorus in the florets and bracts of shrubs fertilized with PAS are of the same order as for shrubs prior to fertilization. However, levels were lower in shrubs fertilized with PU and unfertilized shrubs.

As with shrubs prior to the application of inorganic fertilizers (Figure 3.17a), leaf and stem potassium concentrations of shrubs grown under each of the fertilizer regimes (Figures 5.12a, b and c) were of the same order and did not show seasonal variations during the year. There were, however, seasonal variations in floret and bract potassium

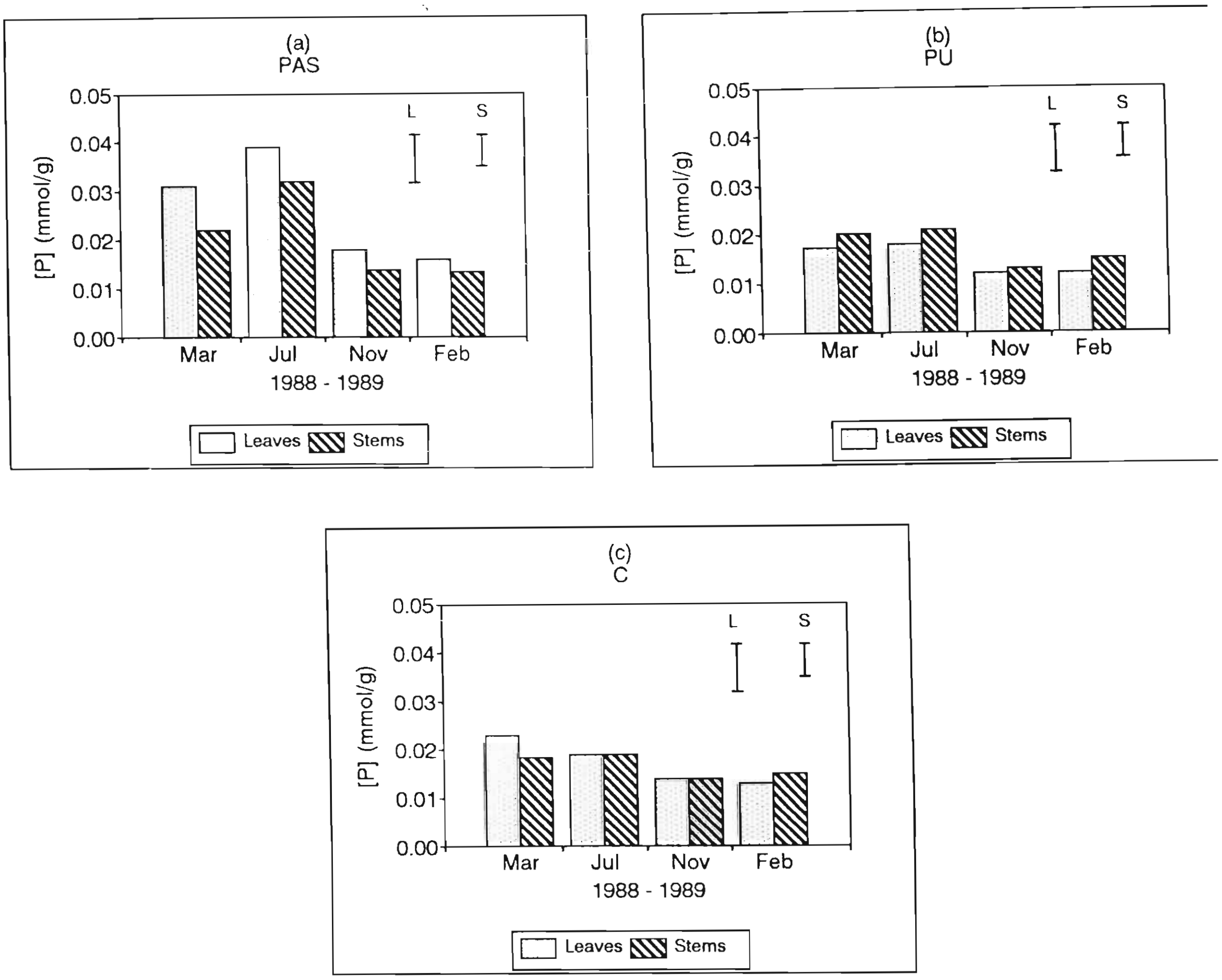


Figure 5.10 Seasonal variation in phosphorus concentration in leaves and stems of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: (a) Plantosan plus ammonium sulphate (PAS), (b) Plantosan plus urea (PU), and (c) unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

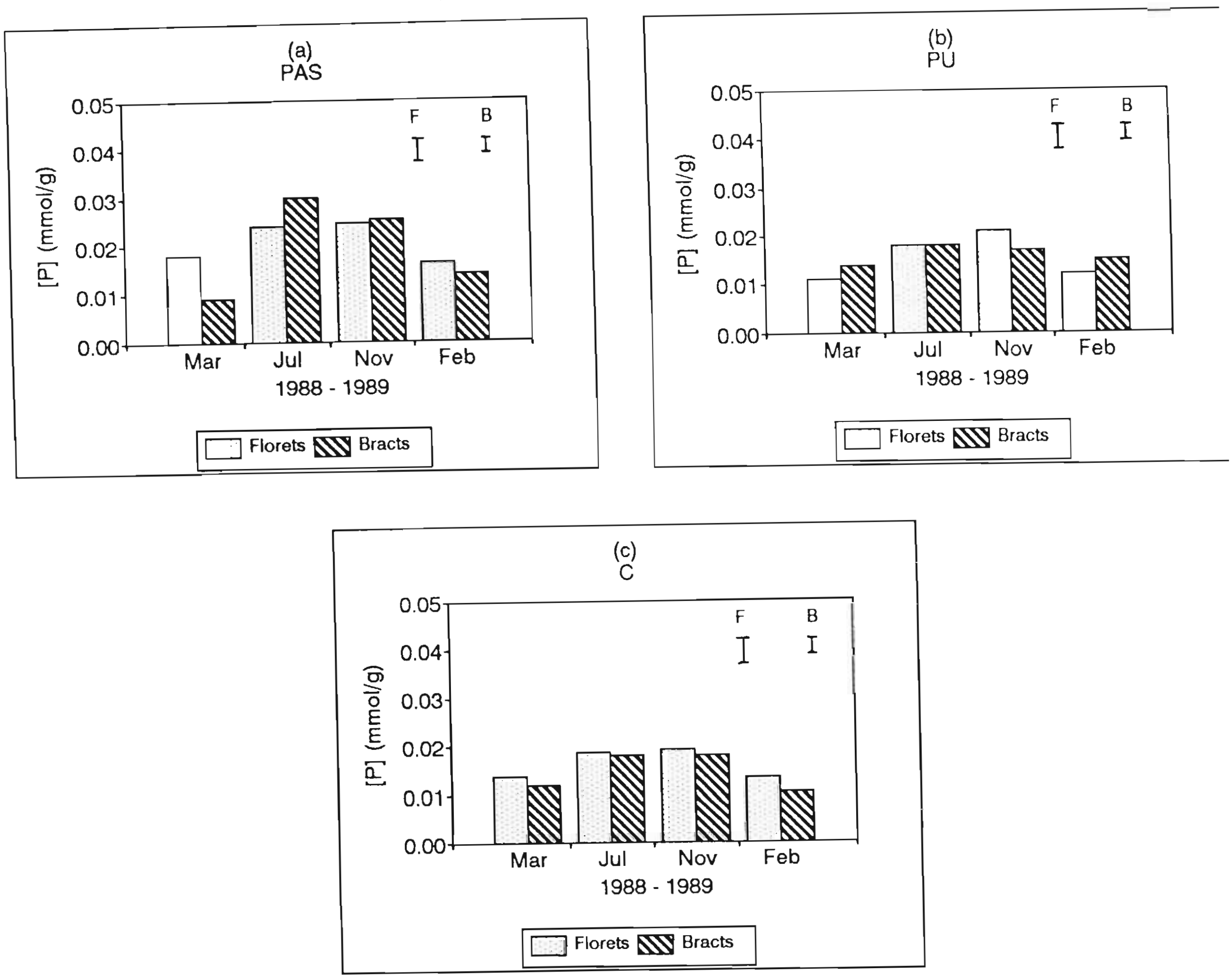


Figure 5.11 Seasonal variation in phosphorus concentration in florets and bracts of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: (a) Plantosan plus ammonium sulphate (PAS), (b) Plantosan plus urea (PU), and (c) unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

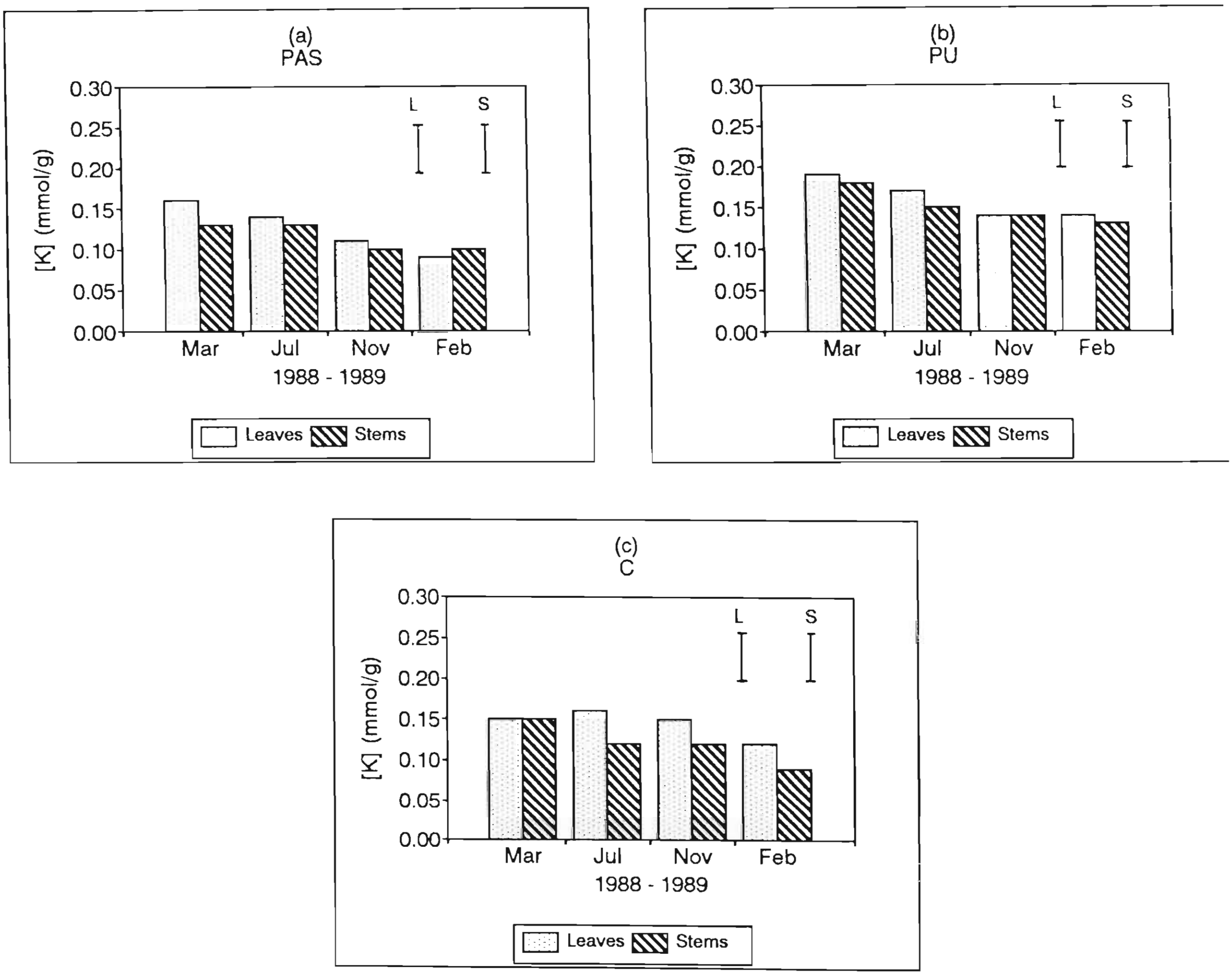


Figure 5.12 Seasonal variation in potassium concentration in leaves and stems of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: (a) Plantosan plus ammonium sulphate (PAS), (b) Plantosan plus urea (PU), and (c) unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

levels of shrubs fertilized with PU (Figure 5.13b), although in shrubs fertilized with PAS (Figure 5.13a) and unfertilized shrubs (Figure 5.13c) these seasonal trends were significant only for bract potassium levels ie. floret potassium levels in these two treatments did not exhibit statistically significant seasonal variation. In general, the highest floret and bract potassium concentration was recorded in July and November (winter/spring) and lowest levels occurred between February and March (late summer/autumn). Furthermore, potassium levels in florets of shrubs fertilized with PU (Figure 5.13b) were greater than potassium levels in florets of shrubs fertilized with PAS and unfertilized shrubs (Figures 5.13a and c), and greater than potassium levels in shrubs prior to the application of inorganic fertilizers (Figure 3.17b). Bract potassium levels were of the same order for each of the three fertilizer treatments (Figures 5.13a, b and c).

The mean nitrogen, phosphorus and potassium concentrations of proteoid and non-proteoid roots of *P. neriifolia* cultivated under different fertilizer regimes are shown in Table 5.7. There are no significant differences between the nitrogen concentration of proteoid roots between shrubs grown under different fertilizer regimes. However, shrubs receiving PU had a non-proteoid root nitrogen concentration significantly higher than for shrubs receiving PAS or shrubs not fertilized. The nitrogen concentration of proteoid roots was higher than that of non-proteoid roots, irrespective of the fertilizer regime under which the shrubs were grown.

There were no significant differences between the phosphorus concentration of proteoid and non-proteoid roots between shrubs grown under different fertilizer regimes. However, the phosphorus concentration of proteoid roots was significantly higher than the phosphorus concentration of non-proteoid roots.

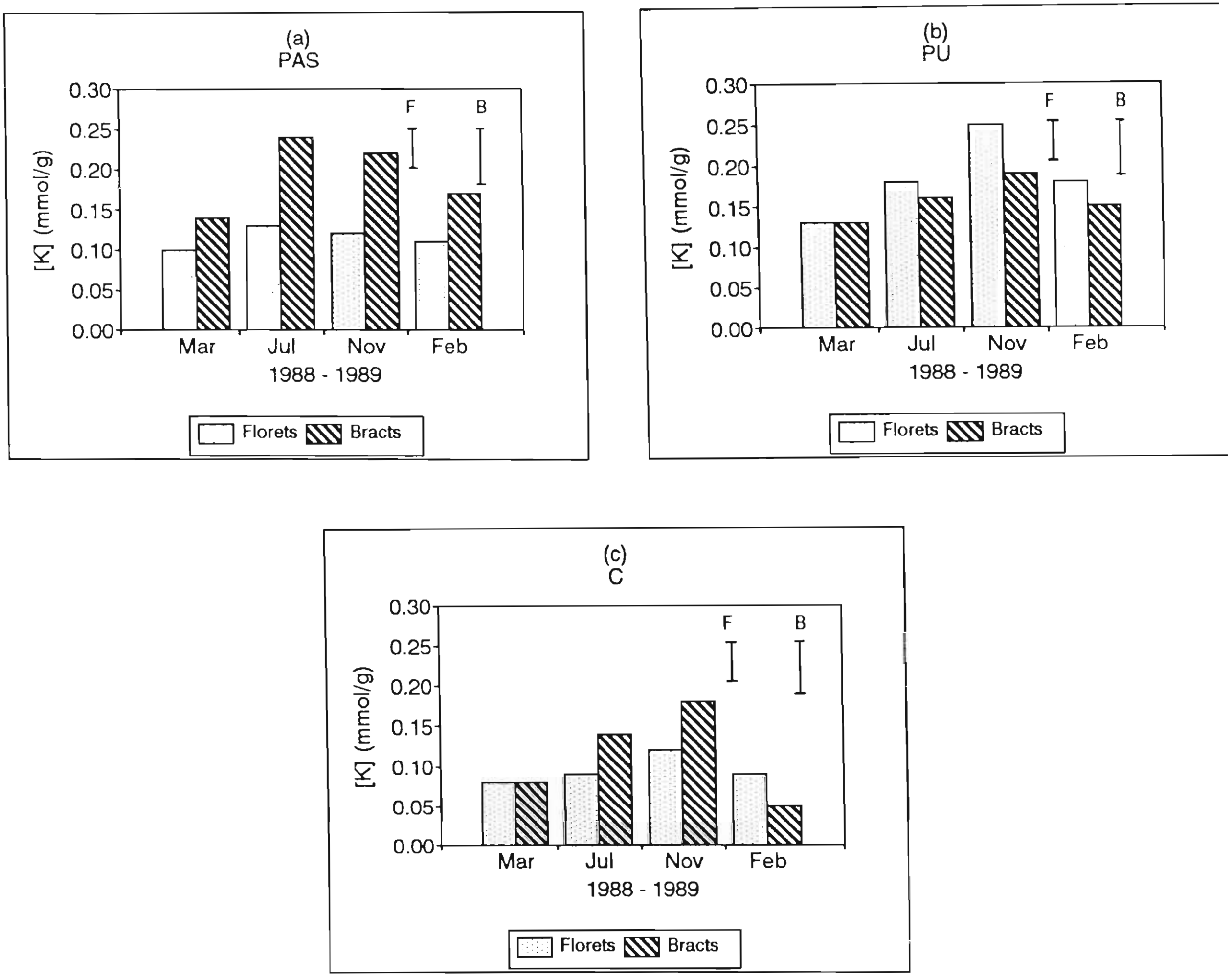


Figure 5.13 Seasonal variation in potassium concentration in florets and bracts of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: (a) Plantosan plus ammonium sulphate (PAS), (b) Plantosan plus urea (PU), and (c) unfertilized control shrubs (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

Table 5.7 Nitrogen, phosphorus and potassium concentration of proteoid and non-proteoid roots of *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). Values are the means of 10 replicates.

	Proteoid roots (mmol g^{-1})			**Non-proteoid roots (mmol g^{-1})**		
	PAS	**PU**	**C**	**PAS**	**PU**	**C**
Nitrogen	0.716^a	0.676^a	0.602^a	0.354^a	0.508^b	0.299^a
Phosphorus	0.014^a	0.010^a	0.011^a	0.004^a	0.004^a	0.005^a
Potassium	0.062^a	0.054^a	0.060^a	0.050^a	0.046^a	0.054^a

Within any one parameter, values followed by different letters are significantly different ($P \leq 0.05$).

The potassium concentration of proteoid and non-proteoid roots was of the same order and there were no differences in potassium root (proteoid and non-proteoid) concentrations between shrubs grown under different fertilizer regimes (Table 5.7).

5.4.2 **Soil nutrient status**

Table 5.8 shows data on the mineral concentration of soils in which *P. neriifolia* was cultivated under different inorganic fertilizer regimes. In comparison with soil nutrient status prior to the application of inorganic fertilizers (Table 2.1), statistical analysis shows that there has been little change in the concentration of the major cations: sodium, potassium (available and total), calcium and magnesium, irrespective of fertilizer applications. However, available phosphorus levels do appear to have increased slightly through the application of Plantosan (PAS and PU) and have remained constant in unfertilized control areas (C). Similarly, soluble nitrogen appears to have increased with inorganic fertilization, particularly with the application of PU. Total nitrogen levels remained relatively constant with fertilization, but in unfertilized control areas, total nitrogen declined significantly. Soil pH has remained relatively constant with a slight decrease being recorded in soils amended with PU.

Changes in soluble nitrogen, total nitrogen, available phosphorus and available potassium are more clearly shown in Figures 5.14a, b, c and d, respectively where seasonal variations in concentration of the nutrients are illustrated. Both soluble (Figure 5.14a) and total (Figure 5.14b) nitrogen are present at the highest level between October and February (spring/summer) and at the lowest level between March and July (autumn/winter). This is similar to the pattern of soluble nitrogen seasonality in soils prior to the application of inorganic fertilizers (Figure 3.18a). Furthermore, the influence of inorganic fertilizers on

Table 5.8 Mineral concentration of the soils of the Mount Sheba Nature Reserve protea cultivation site during the growth of *P. neriifolia* under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). Values are the means (± one standard deviation) of 63 replicates taken over two years. [Data from Table 2.1 for soils prior to fertilization are also shown].

Mineral		**PAS**	**PU**	**C**	**Pre-fert.**
Sodium	mmol kg^{-1}	0.57 ± 0.19	0.17 ± 0.19	0.57 ± 0.16	0.44 ± 0.27
Potassium - total	mmol kg^{-1}	8.80 ± 1.38	8.80 ± 1.38	8.80 ± 1.38	8.80 ± 1.38
Potassium - avail	mmol kg^{-1}	1.09 ± 0.29	1.23 ± 0.25	1.01 ± 0.21	1.19 ± 0.35
Calcium	mmol kg^{-1}	1.19 ± 0.69	1.04 ± 0.66	0.88 ± 0.34	1.60 ± 0.87
Magnesium	mmol kg^{-1}	0.85 ± 0.41	1.05 ± 0.54	1.05 ± 0.57	1.07 ± 0.40
CEC[a]	me 100 g^{-1}	0.68 ± 0.21	0.71 ± 0.28	0.69 ± 0.26	0.69 ± 0.29
Phosphorus - total	mmol kg^{-1}	2.26 ± 0.63	2.26 ± 0.63	2.26 ± 0.63	2.26 ± 0.63
Phosphorus - avail	mmol kg^{-1}	0.46 ± 0.23	0.47 ± 0.14	0.35 ± 0.18	0.35 ± 0.11
Nitrogen - total	mmol kg^{-1}	85.7 ± 14.3[b]	107.1 ± 28.6[c]	64.3 ± 21.4[d]	100.0 ± 21.4[e]
Nitrogen - avail	mmol kg^{-1}	1.87 ± 0.42	2.31 ± 0.36	1.40 ± 0.70	1.68 ± 0.47
pH (water)		4.77 ± 0.42	4.65 ± 0.40	4.80 ± 0.26	4.85 ± 0.47

[a] cation exchange capacity.

[b] - 0.12%.

[c] - 0.15%.

[d] - 0.09%.

[e] - 0.14%.

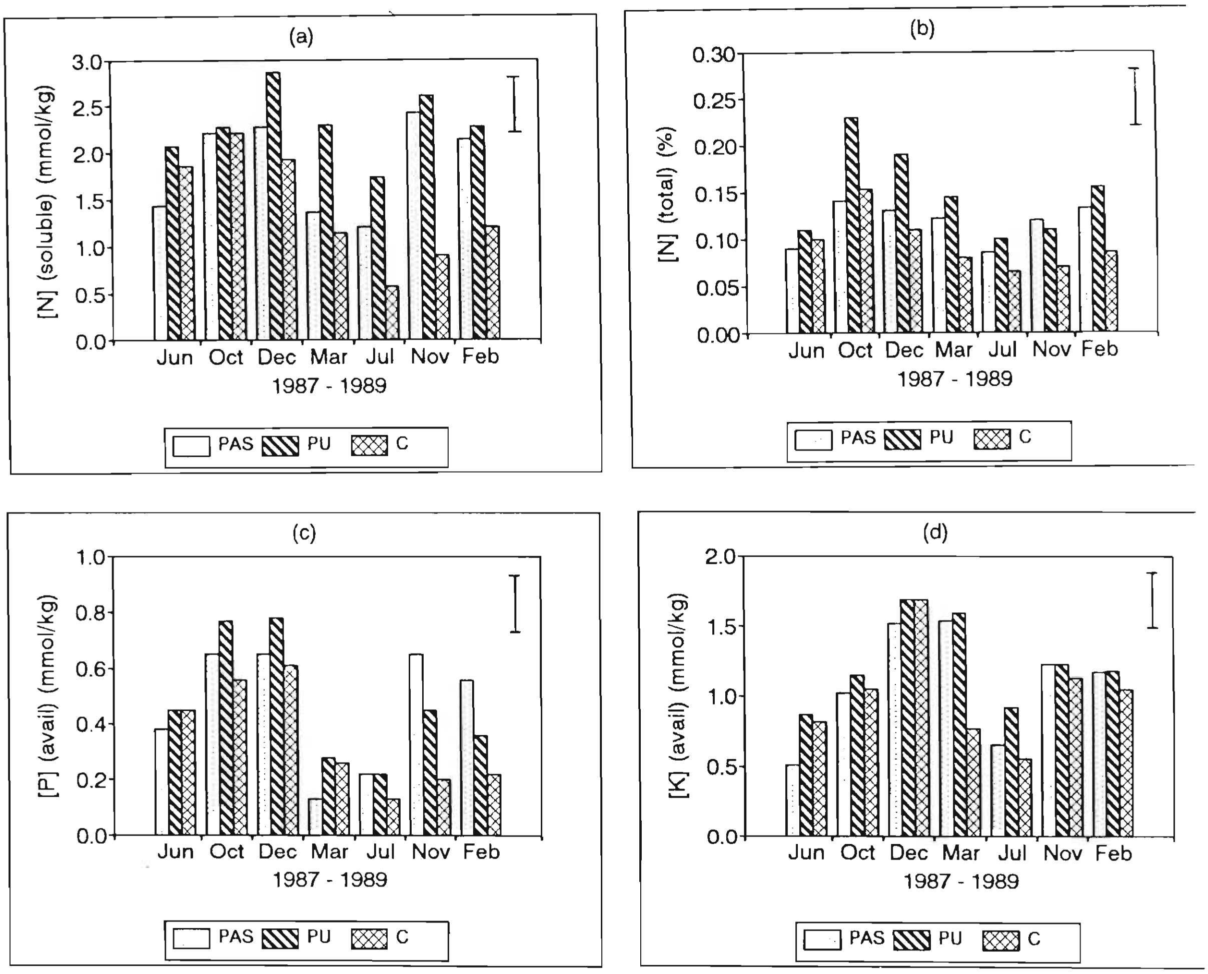


Figure 5.14 Seasonal variation in (a) soluble nitrogen, (b) total nitrogen, (c) available phosphorus, and (d) available potassium concentration of the soils of the Mount Sheba Nature Reserve study site after amendment with either Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), or no amendment (C). The isolated bar represents the minimum significant difference ($P \leq 0.05$). Differences greater than the MSD are statistically significant.

soil nitrogen levels can be seen by the consistently lower levels of soluble and total nitrogen recorded in unfertilized soils, particularly in the latter months of 1988 and the early months of 1989, 18 to 22 months after the initial fertilizer applications. Available phosphorus showed the highest concentration between June and February (winter/spring/ summer) with a low between March and July (autumn/winter) (Figure 5.14c). This is similar to the trend in phosphorus availability in soils prior to the application of inorganic fertilizers (Figure 3.18b), and as with nitrogen, the positive influence of inorganic fertilizers can be seen in the latter months of the trial when soil available phosphorus in unfertilized soils appears to become depleted. Soil available potassium levels (Figure 5.14d) are of the same order irrespective of the application of inorganic fertilizers. Soil available potassium levels appear greatest between October and March (spring/summer/early autumn) with a low between June and July (winter). Again this is similar to soils prior to fertilization (Figure 3.18c). There did not appear to be any change in total levels of soil P and K for the duration of the study.

Therefore, seasonal variations in soluble and total nitrogen, available phosphorus and available potassium did not appear to change significantly with the application of inorganic fertilizers, with greatest availability generally during the wetter months of the year. However, the two fertilizer types did result in the maintenance or increase in soil nitrogen (soluble and total) and phosphorus (available) levels, with unfertilized soils showing depletion of these two nutrients. Soil potassium levels (available) were relatively constant irrespective of fertilization.

5.4.3 The chemical composition of rainwater, shrub throughfall, stemflow, and stream-water

Rainwater and stream-water data presented here are the same as presented in Table 3.6. Shrub throughfall and stemflow data for

Table 5.9 The chemical composition of rainwater, shrub throughfall, stemflow, and stream-water for *P. neriifolia* cultivated in a summer rainfall area under different inorganic fertilizer regimes: Plantosan plus ammonium sulphate (PAS), Plantosan plus urea (PU), and unfertilized control shrubs (C). Values are the means (± one standard deviation) of November 1988 and February 1989 samples replicated as described in Section 2.4.3

		Rainwater	**Shrub throughfall**	**Shrub stemflow**	**Stream-water**
PAS	-N μmol l^{-1}	57.1 ± 20.38	57.1 ± 13.46	57.1 ± 15.23	50.0 ± 4.21
	-P μmol l^{-1}	1.3 ± 0.02	6.4 ± 0.98	6.0 ± 1.12	3.1 ± 0.38
	-K μmol l^{-1}	17.9 ± 0.70	81.8 ± 14.72	79.2 ± 23.67	17.9 ± 0.92
PU	-N μmol l^{-1}	57.1 ± 20.38	57.1 ± 16.35	53.7 ± 23.12	50.0 ± 4.21
	-P μmol l^{-1}	1.3 ± 0.02	6.1 ± 1.12	5.9 ± 2.16	3.1 ± 0.38
	-K μmol l^{-1}	17.9 ± 0.70	64.8 ± 10.45	59.3 ± 8.43	17.9 ± 0.92
C	-N μmol l^{-1}	57.1 ± 20.38	42.8 ± 16.83	48.8 ± 18.27	50.0 ± 4.21
	-P μmol l^{-1}	1.3 ± 0.02	3.1 ± 0.78	3.0 ± 0.86	3.1 ± 0.38
	-K μmol l^{-1}	17.9 ± 0.70	60.1 ± 7.54	59.2 ± 6.91	17.9 ± 0.92

unfertilized shrubs (C) are also the same as that presented in Table 3.6. For clarity, these data are presented again, alongside throughfall and stemflow data for fertilized shrubs (PAS and PU), in Table 5.9.

As described in Section 3.4.3, the concentration of nitrogen (57.1 μmol l^{-1}) in rainwater was considerably higher than both the concentration of phosphorus (1.3 μmol l^{-1}) and potassium (17.9 μmol l^{-1}) (Tables 3.6 and 5.9). For phosphorus and potassium, however, shrub throughfall and stemflow concentrations were greater than the nutrient concentrations in rainwater, irrespective of the fertilizer treatment (Table 5.9). The phosphorus concentration in throughfall in shrubs fertilized with PAS (6.4 μmol l^{-1}) and PU (6.1 μmol l^{-1}) was double the phosphorus concentration in unfertilized shrubs (3.1 μmol l^{-1}). Although there were differences in the potassium concentration in throughfall between fertilizer treatments, standard deviations are large, and statistical analysis indicates that these differences are not statistically significant. Similarly, although the nitrogen concentration in throughfall of unfertilized shrubs (42.8 μmol l^{-1}) was lower than that for shrubs fertilized with PAS and PU (both 57.1 μmol l^{-1}), the data are variable and the large standard deviations show that these differences are not statistically significant (Table 5.9).

The phosphorus concentration in stemflow in shrubs fertilized with PAS (6.0 μmol l^{-1}) and PU (5.9 μmol l^{-1}) was double the phosphorus concentration in unfertilized shrubs (3.0 μmol l^{-1}) (Table 5.9). Although there were differences in the potassium concentration in stemflow between fertilizer treatments, statistical analysis (particularly for shrubs fertilized with PAS) shows that these differences are not statistically significant. Similarly, although the nitrogen concentration in stemflow of unfertilized shrubs (48.8 μmol l^{-1}) was lower than that for shrubs fertilized with PAS (57.1 μmol l^{-1}) and PU (53.7 μmol l^{-1}), standard deviations are large and statistical analysis shows that these differences are not statistically significant (Table 5.9).

Since throughfall and stemflow include dry matter fallout washed from the shrubs during rainfall, increases in phosphorus and potassium concentration in shrub throughfall and stemflow were probably due to either dry matter washing, the leaching of nutrients from the shrubs, or both.

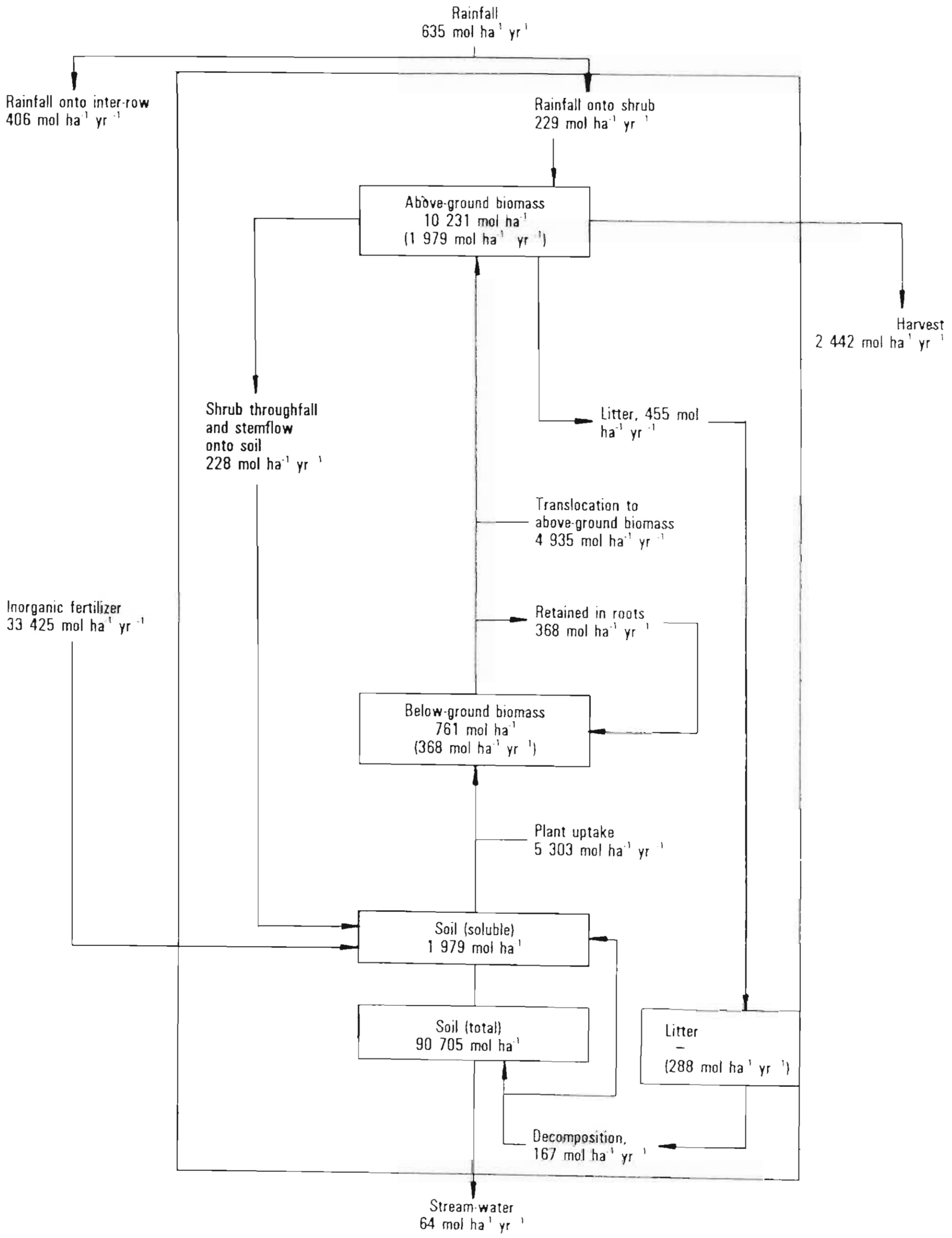
Stream-water analysis (Table 5.9) showed nitrogen levels (50.0 μmol l^{-1}) to be slightly less than the nitrogen concentration in rainfall (57.1 μmol l^{-1}). Stream-water phosphorus concentration (3.1 μmol l^{-1}) was greater than the phosphorus concentration in rainwater (1.3 μmol l^{-1}), while potassium concentrations in stream-water and rainwater were equal (17.9 μmol l^{-1}). Runoff accounts for only 31.8% of rainfall. Therefore, the higher phosphorus concentration in stream-water compared with rainwater suggests that there is some leaching of phosphorus from the soil or parent rock.

5.5 Nutrient cycling and budgets

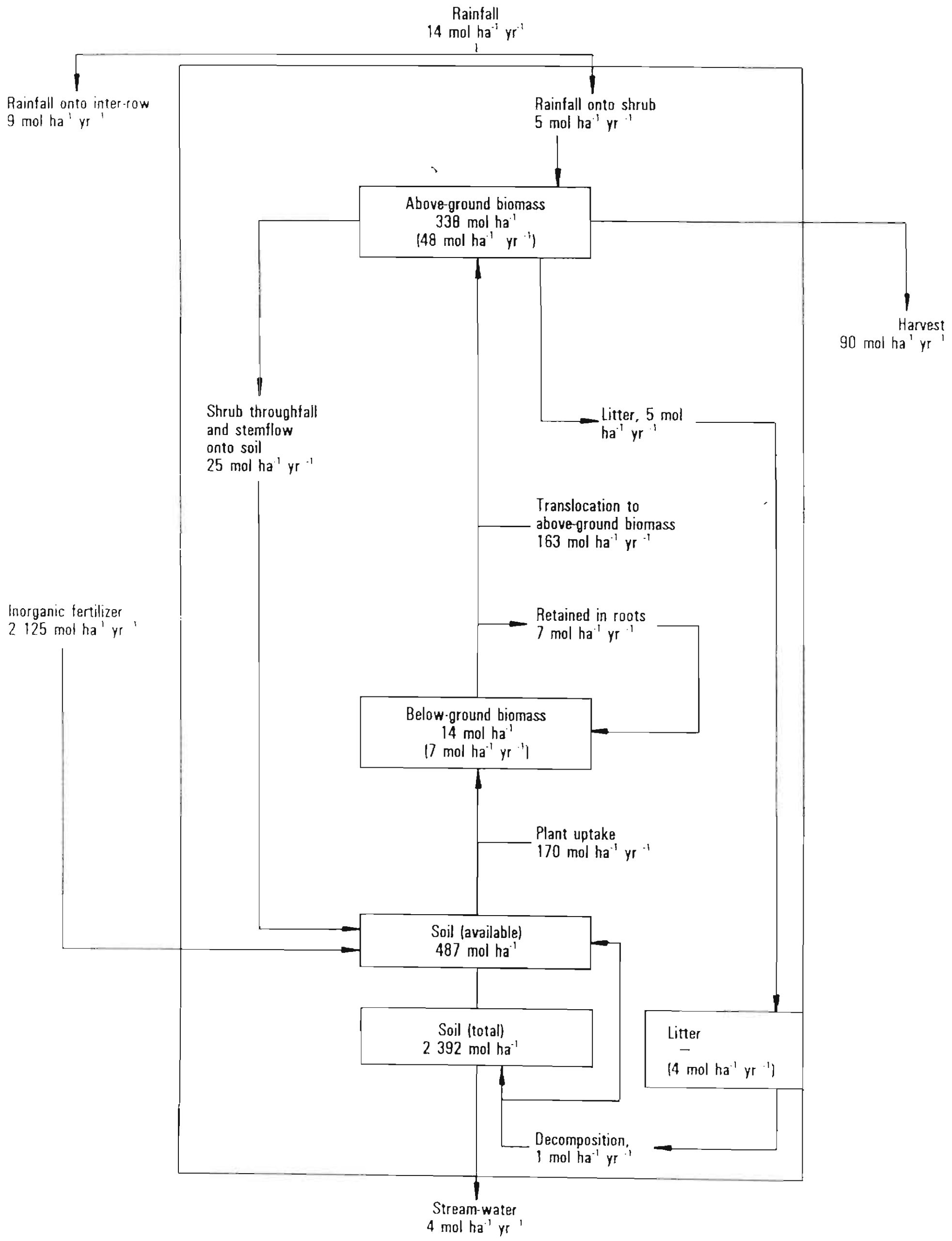
Figures 5.15 (PAS), 5.16 (PU) and 5.17 (C) illustrate nutrient flows and annual budgets for ten year old *P. neriifolia* cultivated in a summer rainfall area under different fertilizer regimes: Plantosan plus ammonium sulphate, Plantosan plus urea, and unfertilized control shrubs, respectively. Data were obtained from the preceding presentation of results and budgets were calculated as described in Section 3.5. The significant difference between budgets presented in Section 3.5 and in Section 5.5 is the inorganic fertilizer input in the latter budgets. This is discussed in Section 5.5.2. Data in the budgets have been converted to express pool sizes as mol ha^{-1} and fluxes as mol ha^{-1} yr^{-1}. Annual increments in pool size are shown in parentheses, and are expressed as mol ha^{-1} yr^{-1}.

Figure 5.15 Annual nutrient budgets (a) nitrogen, (b) phosphorus, and (c) potassium for ten year old *P. neriifolia* cultivated in a summer rainfall area with the application of the inorganic fertilizer, Plantosan plus ammonium sulphate. (Nutrient pools are shown in boxes and the value below the nutrient pool name is the size of the particular nutrient pool. Values in parentheses are annual increments in nutrient pool size, and values on arrows are annual nutrient flux rates.)

(a)


Rainfall 635 mol ha^{-1} yr^{-1}
Rainfall onto inter-row 406 mol ha^{-1} yr^{-1}
Rainfall onto shrub 229 mol ha^{-1} yr^{-1}
Above-ground biomass 10 231 mol ha^{-1} (1 979 mol ha^{-1} yr^{-1})
Harvest 2 442 mol ha^{-1} yr^{-1}
Shrub throughfall and stemflow onto soil 228 mol ha^{-1} yr^{-1}
Litter, 455 mol ha^{-1} yr^{-1}
Translocation to above-ground biomass 4 935 mol ha^{-1} yr^{-1}
Inorganic fertilizer 33 425 mol ha^{-1} yr^{-1}
Retained in roots 368 mol ha^{-1} yr^{-1}
Below-ground biomass 761 mol ha^{-1} (368 mol ha^{-1} yr^{-1})
Plant uptake 5 303 mol ha^{-1} yr^{-1}
Soil (soluble) 1 979 mol ha^{-1}
Soil (total) 90 705 mol ha^{-1}
Litter – (288 mol ha^{-1} yr^{-1})
Decomposition, 167 mol ha^{-1} yr^{-1}
Stream-water 64 mol ha^{-1} yr^{-1}

(b)


Rainfall 14 mol ha^{-1} yr^{-1}
Rainfall onto inter-row 9 mol ha^{-1} yr^{-1}
Rainfall onto shrub 5 mol ha^{-1} yr^{-1}
Above-ground biomass 338 mol ha^{-1} (48 mol ha^{-1} yr^{-1})
Harvest 90 mol ha^{-1} yr^{-1}
Shrub throughfall and stemflow onto soil 25 mol ha^{-1} yr^{-1}
Litter, 5 mol ha^{-1} yr^{-1}
Translocation to above-ground biomass 163 mol ha^{-1} yr^{-1}
Inorganic fertilizer 2 125 mol ha^{-1} yr^{-1}
Retained in roots 7 mol ha^{-1} yr^{-1}
Below-ground biomass 14 mol ha^{-1} (7 mol ha^{-1} yr^{-1})
Plant uptake 170 mol ha^{-1} yr^{-1}
Soil (available) 487 mol ha^{-1}
Soil (total) 2 392 mol ha^{-1}
Litter — (4 mol ha^{-1} yr^{-1})
Decomposition, 1 mol ha^{-1} yr^{-1}
Stream-water 4 mol ha^{-1} yr^{-1}

(c)

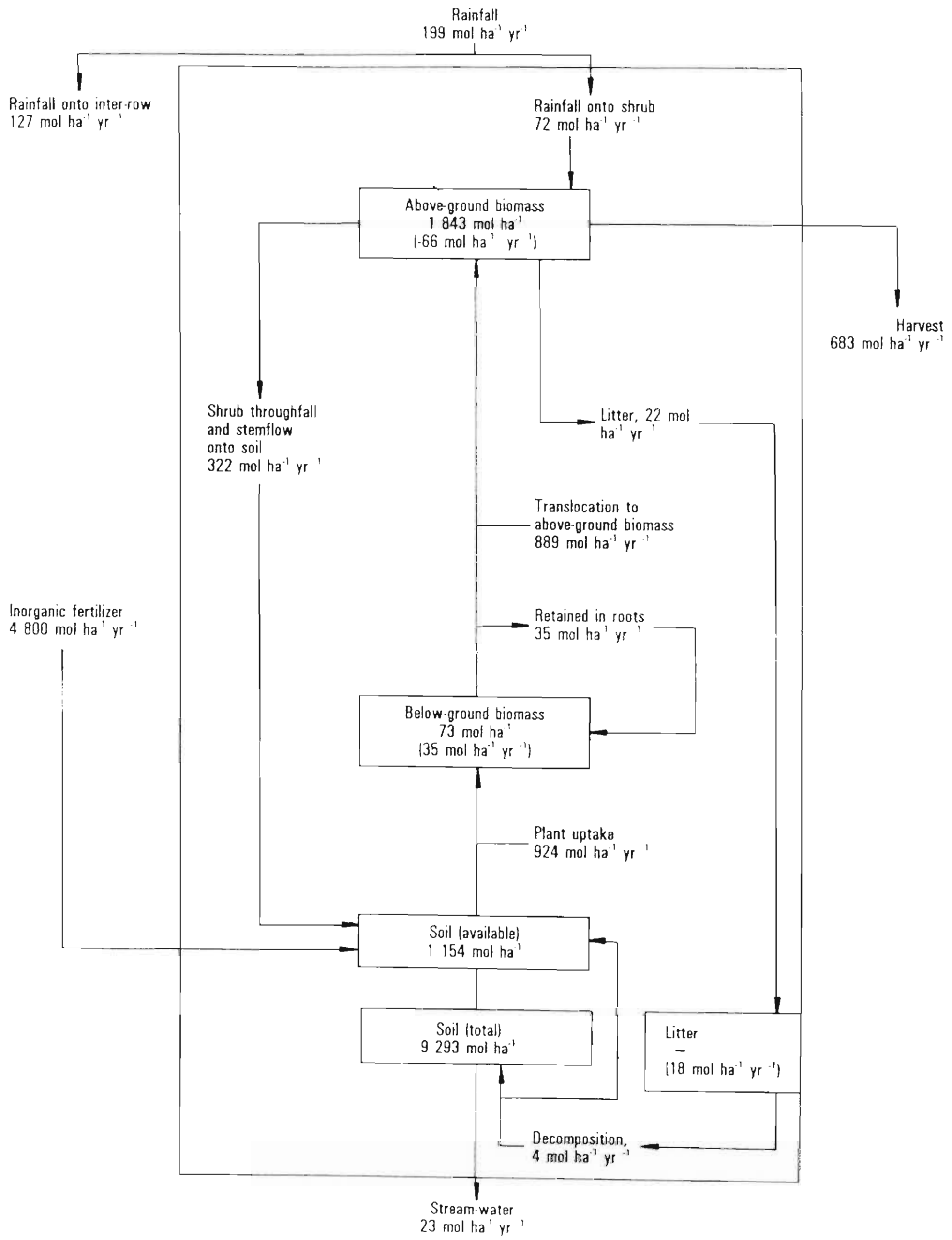
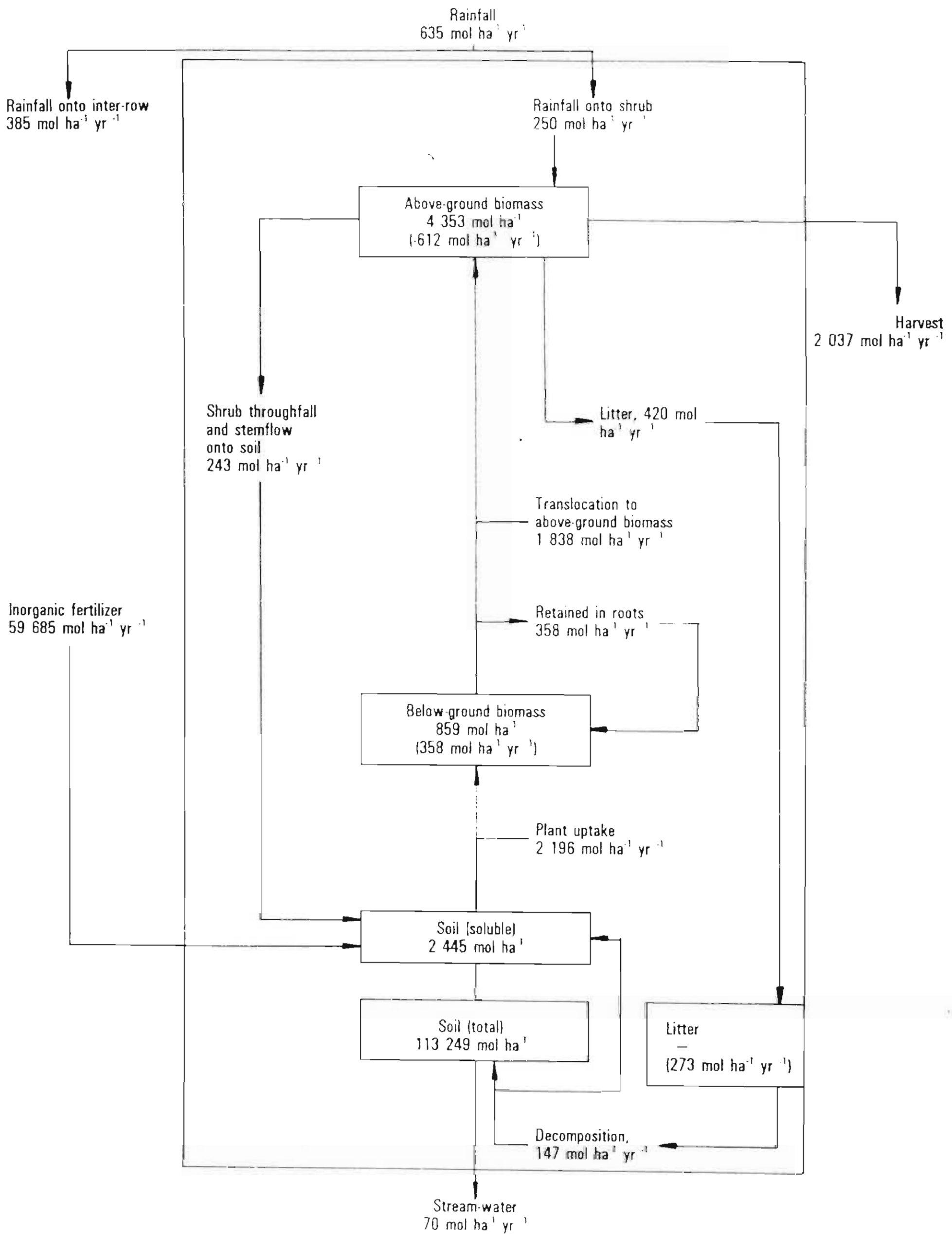
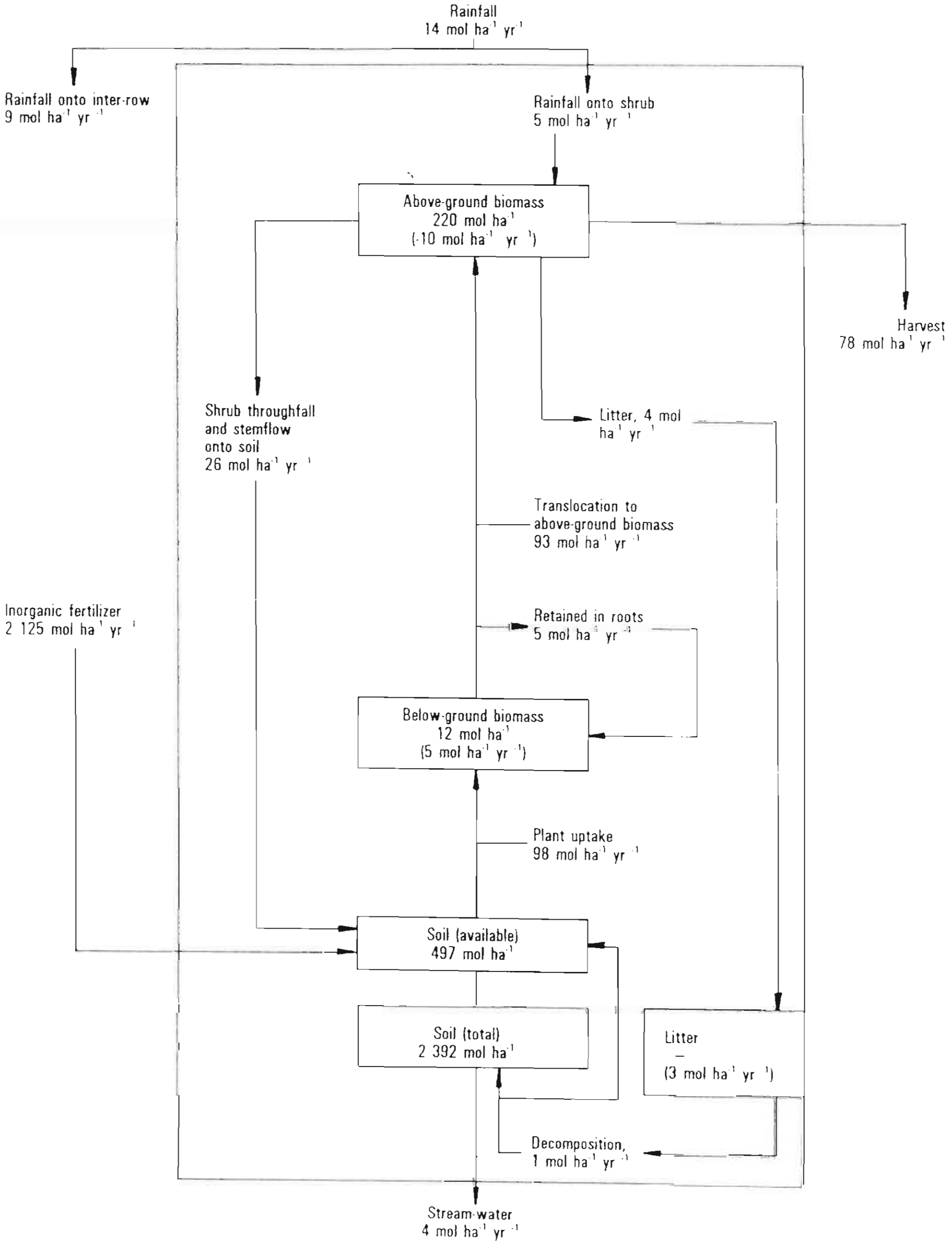

Rainfall
199 mol ha⁻¹ yr⁻¹
Rainfall onto inter-row
127 mol ha⁻¹ yr⁻¹
Rainfall onto shrub
72 mol ha⁻¹ yr⁻¹
Above-ground biomass
1 843 mol ha⁻¹
(-66 mol ha⁻¹ yr⁻¹)
Harvest
683 mol ha⁻¹ yr⁻¹
Shrub throughfall
and stemflow
onto soil
322 mol ha⁻¹ yr⁻¹
Litter, 22 mol
ha⁻¹ yr⁻¹
Translocation to
above-ground biomass
889 mol ha⁻¹ yr⁻¹
Inorganic fertilizer
4 800 mol ha⁻¹ yr⁻¹
Retained in roots
35 mol ha⁻¹ yr⁻¹
Below-ground biomass
73 mol ha⁻¹
(35 mol ha⁻¹ yr⁻¹)
Plant uptake
924 mol ha⁻¹ yr⁻¹
Soil (available)
1 154 mol ha⁻¹
Soil (total)
9 293 mol ha⁻¹
Litter
–
(18 mol ha⁻¹ yr⁻¹)
Decomposition,
4 mol ha⁻¹ yr⁻¹
Stream-water
23 mol ha⁻¹ yr⁻¹

Figure 5.16 Annual nutrient budgets (a) nitrogen, (b) phosphorus, and (c) potassium for ten year old *P. neriifolia* cultivated in a summer rainfall area with the application of the inorganic fertilizer, Plantosan plus urea. (Nutrient pools are shown in boxes and the value below the nutrient pool name is the size of the particular nutrient pool. Values in parentheses are annual increments in nutrient pool size, and values on arrows are annual nutrient flux rates.)

(a)


Rainfall
635 mol ha^{-1} yr^{-1}
Rainfall onto inter-row
385 mol ha^{-1} yr^{-1}
Rainfall onto shrub
250 mol ha^{-1} yr^{-1}
Above-ground biomass
4 353 mol ha^{-1}
(-612 mol ha^{-1} yr^{-1})
Harvest
2 037 mol ha^{-1} yr^{-1}
Shrub throughfall and stemflow onto soil
243 mol ha^{-1} yr^{-1}
Litter, 420 mol ha^{-1} yr^{-1}
Translocation to above-ground biomass
1 838 mol ha^{-1} yr^{-1}
Inorganic fertilizer
59 685 mol ha^{-1} yr^{-1}
Retained in roots
358 mol ha^{-1} yr^{-1}
Below-ground biomass
859 mol ha^{-1}
(358 mol ha^{-1} yr^{-1})
Plant uptake
2 196 mol ha^{-1} yr^{-1}
Soil (soluble)
2 445 mol ha^{-1}
Soil (total)
113 249 mol ha^{-1}
Litter
—
(273 mol ha^{-1} yr^{-1})
Decomposition,
147 mol ha^{-1} yr^{-1}
Stream-water
70 mol ha^{-1} yr^{-1}

(b)


Rainfall 14 mol ha^{-1} yr^{-1}
Rainfall onto inter-row 9 mol ha^{-1} yr^{-1}
Rainfall onto shrub 5 mol ha^{-1} yr^{-1}
Above-ground biomass 220 mol ha^{-1} (-10 mol ha^{-1} yr^{-1})
Harvest 78 mol ha^{-1} yr^{-1}
Shrub throughfall and stemflow onto soil 26 mol ha^{-1} yr^{-1}
Litter, 4 mol ha^{-1} yr^{-1}
Translocation to above-ground biomass 93 mol ha^{-1} yr^{-1}
Inorganic fertilizer 2 125 mol ha^{-1} yr^{-1}
Retained in roots 5 mol ha^{-1} yr^{-1}
Below-ground biomass 12 mol ha^{-1} (5 mol ha^{-1} yr^{-1})
Plant uptake 98 mol ha^{-1} yr^{-1}
Soil (available) 497 mol ha^{-1}
Soil (total) 2 392 mol ha^{-1}
Litter – (3 mol ha^{-1} yr^{-1})
Decomposition, 1 mol ha^{-1} yr^{-1}
Stream-water 4 mol ha^{-1} yr^{-1}

(c)

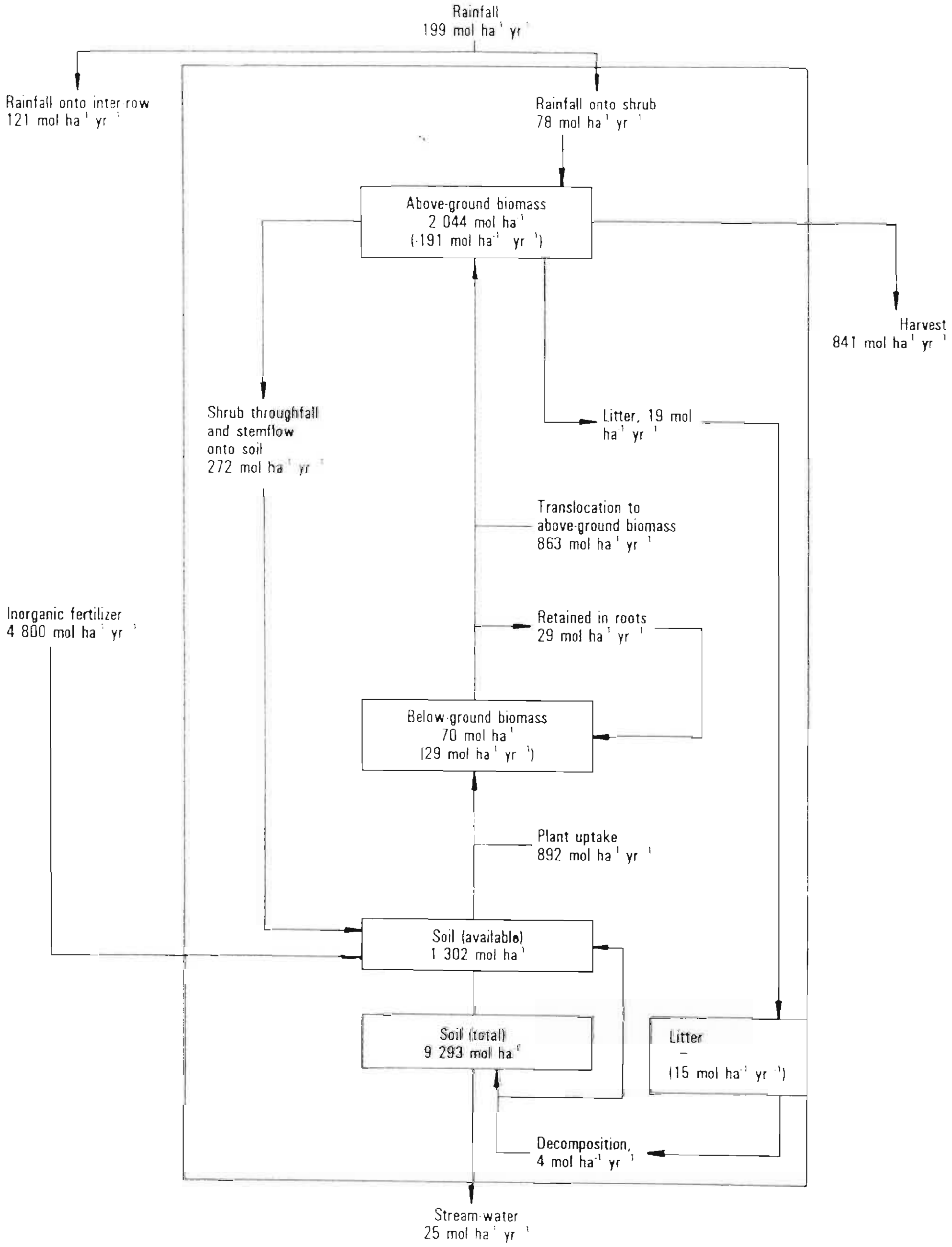
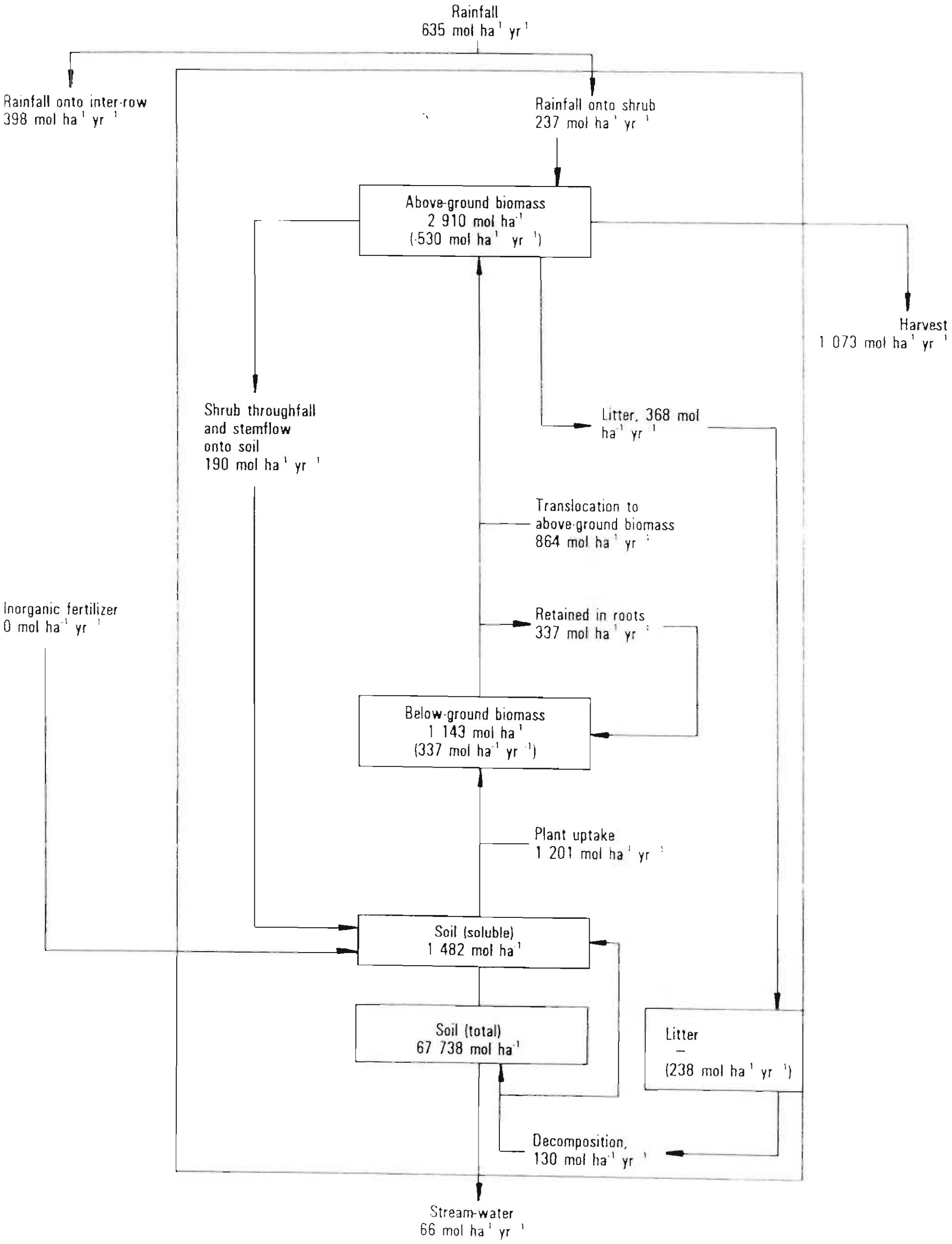

Rainfall
199 mol ha^{-1} yr^{-1}
Rainfall onto inter-row
121 mol ha^{-1} yr^{-1}
Rainfall onto shrub
78 mol ha^{-1} yr^{-1}
Above-ground biomass
2 044 mol ha^{-1}
(-191 mol ha^{-1} yr^{-1})
Harvest
841 mol ha^{-1} yr^{-1}
Shrub throughfall
and stemflow
onto soil
272 mol ha^{-1} yr^{-1}
Litter, 19 mol
ha^{-1} yr^{-1}
Translocation to
above-ground biomass
863 mol ha^{-1} yr^{-1}
Inorganic fertilizer
4 800 mol ha^{-1} yr^{-1}
Retained in roots
29 mol ha^{-1} yr^{-1}
Below-ground biomass
70 mol ha^{-1}
(29 mol ha^{-1} yr^{-1})
Plant uptake
892 mol ha^{-1} yr^{-1}
Soil (available)
1 302 mol ha^{-1}
Soil (total)
9 293 mol ha^{-1}
Litter
–
(15 mol ha^{-1} yr^{-1})
Decomposition,
4 mol ha^{-1} yr^{-1}
Stream-water
25 mol ha^{-1} yr^{-1}

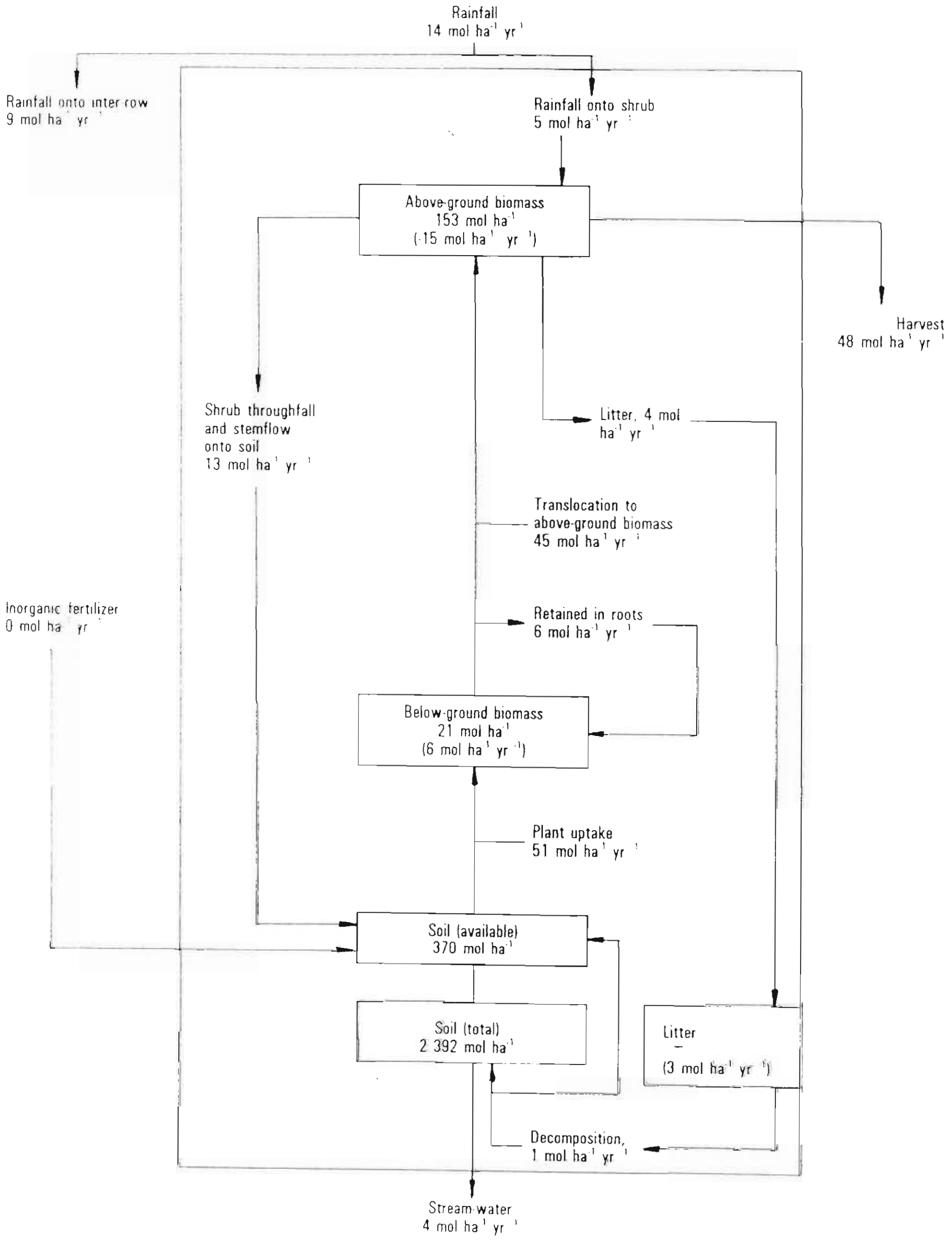
Figure 5.17 Annual nutrient budgets (a) nitrogen, (b) phosphorus, and (c) potassium for ten year old *P. neriifolia* cultivated in a summer rainfall area without the application of inorganic fertilizers. (Nutrient pools are shown in boxes and the value below the nutrient pool name is the size of the particular nutrient pool. Values in parentheses are annual increments in nutrient pool size, and values on arrows are annual nutrient flux rates.)

(a)

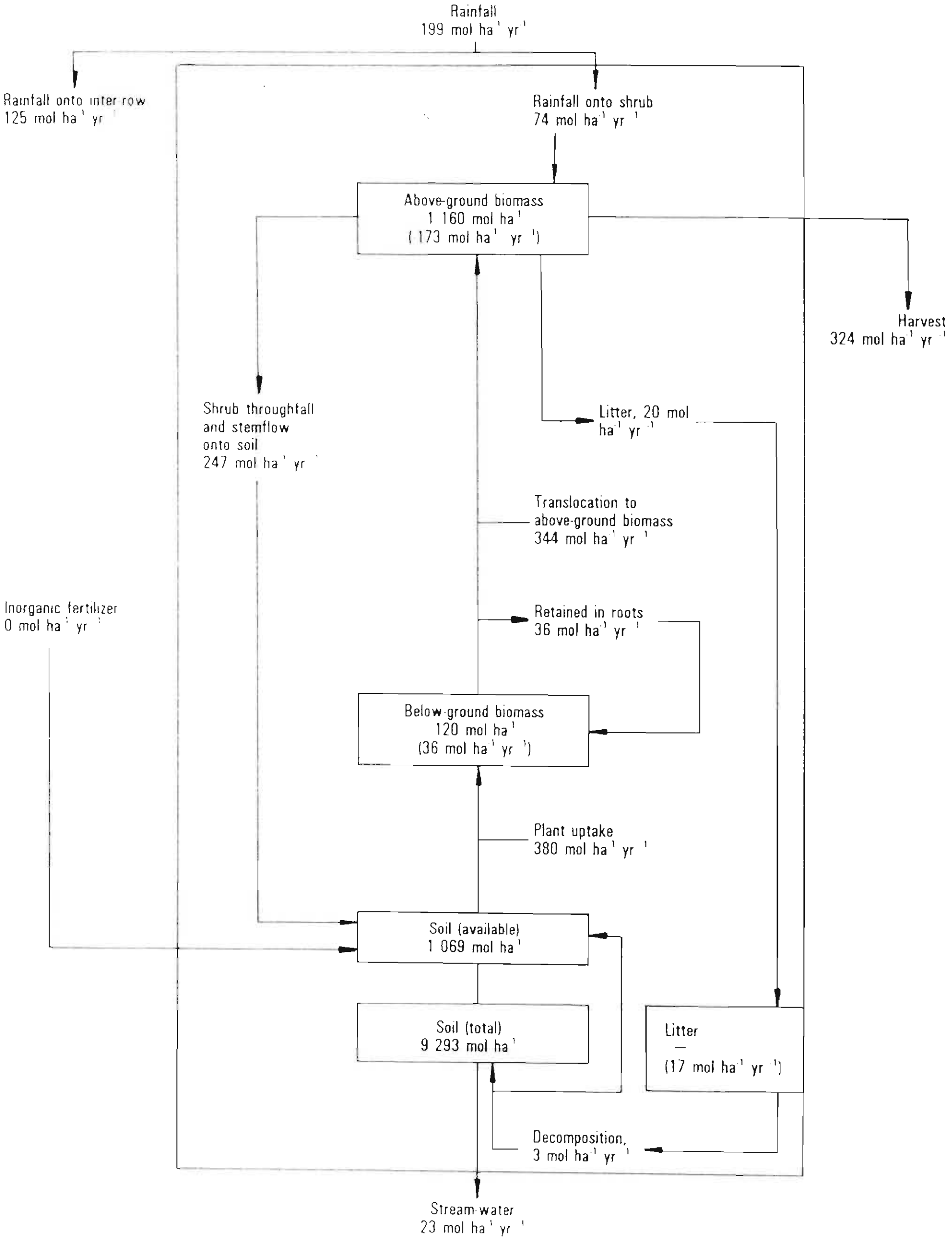


Rainfall
635 mol ha^{-1} yr^{-1}
Rainfall onto inter-row
398 mol ha^{-1} yr^{-1}
Rainfall onto shrub
237 mol ha^{-1} yr^{-1}
Above-ground biomass
2 910 mol ha^{-1}
(-530 mol ha^{-1} yr^{-1})
Harvest
1 073 mol ha^{-1} yr^{-1}
Shrub throughfall
and stemflow
onto soil
190 mol ha^{-1} yr^{-1}
Litter, 368 mol
ha^{-1} yr^{-1}
Translocation to
above-ground biomass
864 mol ha^{-1} yr^{-1}
Inorganic fertilizer
0 mol ha^{-1} yr^{-1}
Retained in roots
337 mol ha^{-1} yr^{-1}
Below-ground biomass
1 143 mol ha^{-1}
(337 mol ha^{-1} yr^{-1})
Plant uptake
1 201 mol ha^{-1} yr^{-1}
Soil (soluble)
1 482 mol ha^{-1}
Soil (total)
67 738 mol ha^{-1}
Litter
–
(238 mol ha^{-1} yr^{-1})
Decomposition,
130 mol ha^{-1} yr^{-1}
Stream-water
66 mol ha^{-1} yr^{-1}

(b)


Rainfall
14 mol ha^{-1} yr^{-1}
Rainfall onto inter row
9 mol ha^{-1} yr^{-1}
Rainfall onto shrub
5 mol ha^{-1} yr^{-1}
Above-ground biomass
153 mol ha^{-1}
(-15 mol ha^{-1} yr^{-1})
Harvest
48 mol ha^{-1} yr^{-1}
Shrub throughfall and stemflow onto soil
13 mol ha^{-1} yr^{-1}
Litter, 4 mol ha^{-1} yr^{-1}
Translocation to above-ground biomass
45 mol ha^{-1} yr^{-1}
Inorganic fertilizer
0 mol ha^{-1} yr^{-1}
Retained in roots
6 mol ha^{-1} yr^{-1}
Below-ground biomass
21 mol ha^{-1}
(6 mol ha^{-1} yr^{-1})
Plant uptake
51 mol ha^{-1} yr^{-1}
Soil (available)
370 mol ha^{-1}
Soil (total)
2 392 mol ha^{-1}
Litter
–
(3 mol ha^{-1} yr^{-1})
Decomposition,
1 mol ha^{-1} yr^{-1}
Stream-water
4 mol ha^{-1} yr^{-1}

(c)


Rainfall 199 mol ha^{-1} yr^{-1}
Rainfall onto inter row 125 mol ha^{-1} yr^{-1}
Rainfall onto shrub 74 mol ha^{-1} yr^{-1}
Above-ground biomass 1 160 mol ha^{-1} (173 mol ha^{-1} yr^{-1})
Harvest 324 mol ha^{-1} yr^{-1}
Shrub throughfall and stemflow onto soil 247 mol ha^{-1} yr^{-1}
Litter, 20 mol ha^{-1} yr^{-1}
Translocation to above-ground biomass 344 mol ha^{-1} yr^{-1}
Inorganic fertilizer 0 mol ha^{-1} yr^{-1}
Retained in roots 36 mol ha^{-1} yr^{-1}
Below-ground biomass 120 mol ha^{-1} (36 mol ha^{-1} yr^{-1})
Plant uptake 380 mol ha^{-1} yr^{-1}
Soil (available) 1 069 mol ha^{-1}
Soil (total) 9 293 mol ha^{-1}
Litter — (17 mol ha^{-1} yr^{-1})
Decomposition, 3 mol ha^{-1} yr^{-1}
Stream-water 23 mol ha^{-1} yr^{-1}

In each case, more nitrogen was cycled than potassium which, in turn, was greater than phosphorus. Furthermore, the annual nitrogen and phosphorus budgets of shrubs receiving PAS were larger than those for shrubs receiving PU, which were larger than those for shrubs not fertilized (C). Annual potassium budgets for shrubs receiving either PAS or PU were of the same order but larger than the annual potassium budget of unfertilized shrubs (C).

5.5.1 **Nutrient pools**

The nitrogen pool in the above-ground biomass of shrubs fertilized with PAS (Figure 5.15a) was approximately 2.5 times greater than that for shrubs receiving PU (Figure 5.16a) and 3.5 times greater than that of unfertilized shrubs (Figure 5.17a). In contrast, however, the nitrogen pool in the below-ground biomass was highest in unfertilized shrubs (Figure 5.17a) followed by shrubs receiving PU (Figure 5.16a). The lowest below-ground nitrogen pool was recorded for shrubs with the largest above-ground nitrogen pool viz. shrubs receiving PAS (Figure 5.15a). Soil total nitrogen pool size ranged from 67 738 to 113 249 mol ha^{-1}, and soil soluble pool size ranged from 1 482 to 2 445 mol ha^{-1}, being highest in areas where PU was applied (Figure 5.16b). The size of all nitrogen pools for ten year old shrubs, either fertilized or unfertilized, (except the soil nitrogen pool (soluble and total) for unfertilized shrubs) was larger than the respective pool sizes for seven year old shrubs prior to the application of inorganic fertilizers (Figure 3.19a).

Phosphorus pool sizes followed a similar trend to those for nitrogen. The phosphorus pool in the above-ground biomass of shrubs fertilized with PAS (Figure 5.15b) was 1.5 times greater than that for shrubs receiving PU (Figure 5.16b) and more than twice that of unfertilized shrubs (Figure 5.17b). The phosphorus pool in the below-ground biomass was greatest in the unfertilized control shrubs (Figure 5.17b), almost double the size of phosphorus pools in the below-ground biomass of both PAS and PU fertilized shrubs (Figures 5.15b and 5.16b). Soil phosphorus (available and total) pool sizes were of the same order, with levels being slightly higher for those shrubs receiving inorganic fertilizers (Figures 5.15b and 5.16b). All phosphorus pool sizes (except total soil P pool size) for each of the three fertilizer treatments were larger than those for shrubs prior to the application of inorganic fertilizers (Figure 3.19b).

The potassium pools in the above- and below-ground biomass for shrubs fertilized with PAS (Figure 5.15c) and PU (Figure 5.16c) were similar. However, the potassium pool in the above-ground biomass of these shrubs was 1.5 times greater than that for unfertilized shrubs (Figure 5.17c). In contrast, however, the potassium pool in the below-ground biomass of unfertilized shrubs (Figure 5.17c) was 1.5 times greater than that for fertilized shrubs (Figures 5.15c and 5.16c). Soil potassium (available and total) pool sizes were of the same order for both fertilized and unfertilized shrubs. As with nitrogen and phosphorus, potassium pool sizes for each of the three fertilizer treatments (except the soil available potassium pool for unfertilized shrubs) were greater than for shrubs prior to the application of inorganic fertilizers (Figure 3.19c).

In general, therefore, the application of inorganic fertilizers resulted in an increase in the above-ground nutrient pools and a decrease in the below-ground nutrient pools.

The relative contribution of nutrient pools in the above- and below-ground biomass to nutrient pools in the total biomass varied between fertilizer treatments and between minerals. For nitrogen, the nutrient pool in the above-ground biomass contributed 25 times, 5 times and 2.5 times more to the nutrient pool in the total biomass than the nutrient pool in the below-ground biomass for shrubs fertilized with PAS, PU, and unfertilized shrubs, respectively. For phosphorus, the nutrient pool in the above-ground biomass contributed 24 times, 18 times and 7 times more than the nutrient pool in the below-ground biomass for the respective fertilizer treatments; and for potassium, the nutrient pool in the above-ground biomass contributed 25 times, 29 times and 10 times more than the nutrient pool in the below-ground biomass for the respective fertilizer treatments. There does not appear to be a distinct pattern in allocation to nutrient pools in the above- and below-ground biomass. This is supported by the relative contribution of the nutrient pools in the above- and below-ground biomass to the nutrient pool in the total biomass of shrubs prior to the application of inorganic fertilizers viz. 10 times, 27 times and 23 times more for nutrient pools in the above-ground than nutrient pools in the below-ground biomass for nitrogen, phosphorus and potassium, respectively.

5.5.2 Inputs and losses

Unlike shrubs prior to the application of inorganic fertilizers (Section 3.5.2), there were two inputs to the system measured in fertilized shrubs viz. rainfall and inorganic fertilizers. For each fertilizer treatment, nitrogen, phosphorus and potassium input from rainfall was the same (Figures 5.15, 5.16 and 5.17). Rainfall contained 3 times more nitrogen than potassium and 45 times more nitrogen than phosphorus. This is the same as for rainfall prior to the application of inorganic fertilizers (Section 3.5.2).

In shrubs receiving inorganic fertilizers the major nutrient input into the system was from the inorganic fertilizers. In each case Plantosan was supplemented with additional nitrogen. Therefore, nitrogen inputs were considerably higher than both phosphorus and potassium inputs. Furthermore, on a mass basis, urea contains almost double the amount of nitrogen than ammonium sulphate. Therefore, nitrogen input from PU (Figure 5.16a) was almost double the input from PAS (Figure

5.15a). The phosphorus and potassium inputs were the same for both fertilizer treatments (Figures 5.15b and c and 5.16b and c). Nutrient inputs from inorganic fertilizers were calculated from annual delivery rates presented in Table 2.6. However, although budgets are expressed on an hectare basis, inorganic fertilizers were applied to the protea component of the community only. For all nutrients, inputs from inorganic fertilizers were considerably higher than the inputs from rainfall.

There were two major sources of nutrient loss from the system. For each fertilizer treatment the smaller loss occurred through stream-water and for each fertilizer treatment, this loss was the same. Again, it is important to note that as a result of limited rainfall and stream-water data it was not possible to differentiate between the treatments. Nitrogen loss was 3 times greater than potassium loss and 16 times greater than phosphorus loss (Figures 5.15, 5.16 and 5.17). This is the same as stream-water losses prior to the application of inorganic fertilizers (Section 3.5.2).

As with shrubs prior to the application of inorganic fertilizers (Section 3.5.2) the larger loss of nutrients from the system occurred through the harvest of flowers for commercial sale. The annual nitrogen loss through the harvest of flowers was 2 442, 2 037 and 1 073 mol ha^{-1} yr^{-1} for shrubs fertilized with PAS (Figure 5.15a), PU (Figure 5.16a) and unfertilized control shrubs (Figure 5.17a), respectively. The annual phosphorus and potassium losses for the same fertilizer treatments were 90 (Figure 5.15b), 78 (Figure 5.16b) and 48 (Figure 5.17b) mol ha^{-1} yr^{-1}, and 683 (Figure 5.15c), 841 (Figure 5.16c) and 324 (Figure 5.17c) mol ha^{-1} yr^{-1}, respectively. Nitrogen loss is, therefore, greater than potassium loss which is greater than phosphorus loss. In addition, excluding potassium, losses from shrubs fertilized with PAS were greater than losses from shrubs fertilized with PU which, in turn, were greater than losses from unfertilized shrubs. Since the number of flowers produced by shrubs fertilized with either PAS or PU is similar (Table 5.5), differences in loss through flower harvesting reflect the higher nutrient concentration (nitrogen and phosphorus) in flowers of shrubs fertilized with PAS compared to shrubs fertilized with PU (Figures 5.9, 5.11). The greater loss of nutrients from fertilized shrubs compared to unfertilized shrubs reflects both the greater number of flowers produced by fertilized shrubs compared to unfertilized shrubs (Table 5.5), and also the higher nutrient concentration in flowers from fertilized shrubs (Figure 5.9, 5.11 and 5.13), particularly the higher nutrient concentration in flowers from shrubs fertilized with PAS.

For shrubs fertilized with PAS, the loss of nitrogen, phosphorus and potassium through flower harvesting represents 24, 27 and 37%, respectively, of the nutrient pools in the above-ground biomass. For shrubs fertilized with PU this represents 47, 35 and 41%, and for unfertilized shrubs 37, 31 and 28%, respectively. Compared with shrubs prior to the application of inorganic fertilizers (Section 3.5.2), the most favourable balance between increases in nutrient pool sizes in the above-ground biomass and nutrient loss through the harvest of flowers was in shrubs fertilized with PAS, followed by unfertilized shrubs. Although shrubs fertilized with PU showed an increase in the number of flowers produced, this was at the expense of nutrient accumulation in the nutrient pools in the above-ground biomass. Compared with either shrubs fertilized with PAS, or unfertilized shrubs, this resulted in a proportionately lower increase in size in the nutrient pools in the above-ground biomass.

5.5.3 Nutrient flows within the plant/soil system

There were three nutrient flows within the plant/soil system that were studied.

Rainfall flows, either directly on to the shrubs or on to the inter-row, were similar for each of the three fertilizer treatments. Since the volume of rainfall and the nutrient concentration of rainwater were the same for each of the three fertilizer treatments, differences that did occur were the result of shrub canopy area. However, all shrubs (fertilized and unfertilized) intercepted comparable levels of nitrogen, phosphorus and potassium through rainfall (Figures 5.15, 5.16 and 5.17). Similarly, for each of the fertilizer treatments, comparable levels of all nutrients fell on to the inter-row (Figures 5.15, 5.16 and 5.17). The nutrients in rainwater that fell on to the inter-row were unavailable to the *P. neriifolia* shrubs and have been excluded from the budgets. For shrubs fertilized with PAS and PU, shrub throughfall and stemflow nitrogen levels (228 and 243 mol ha^{-1} yr^{-1}, respectively) were similar to nitrogen levels in the rainwater that fell directly on to the shrubs (229 and 250 mol ha^{-1} yr^{-1}, respectively). Therefore, there was no nett absorption or nett loss of nitrogen from fertilized shrubs during rainfall (Figures 5.15a and 5.16a). In contrast, however, unfertilized shrubs did absorb nitrogen, with shrub throughfall and stemflow nitrogen levels (190 mol ha^{-1} yr^{-1}) being lower than nitrogen levels in the rainwater (237 mol ha^{-1} yr^{-1}) (Figure 5.17a). This is similar to gains in the nitrogen pool in the above-ground biomass described for shrubs prior to the application of inorganic fertilizers (Section 3.5.3).

For all fertilizer treatments, phosphorus and potassium shrub throughfall and stemflow levels (25 and 322, 26 and 272, and 13 and 247 mol ha^{-1} yr^{-1} for PAS, PU and C shrubs, respectively) were greater than the respective nutrient levels in rainwater (5 and 72, 5 and 78, and 5 and 74 mol ha^{-1} yr^{-1} for PAS, PU and C shrubs, respectively) (Figures 5.15b and c, 5.16b and c, and 5.17b and c). This suggests a nett loss of phosphorus and potassium from the nutrient pools in the above-ground biomass and a nett gain to the soil.

The flows of nitrogen, phosphorus and potassium through litter production and decomposition were similar for the three nutrients and the three fertilizer treatments studied. Nitrogen loss through litter production from shrubs fertilized with PAS was 455 mol ha^{-1} yr^{-1} (Figure 5.15a). For shrubs fertilized with PU, nitrogen loss through litter production was 420 mol ha^{-1} yr^{-1} (Figure 5.16a) and for unfertilized shrubs, 368 mol ha^{-1} yr^{-1} (Figure 5.17a). Decomposition and return of nitrogen to the soil was of the same order for each of the fertilizer treatments viz. 167, 147 and 130 mol ha^{-1} yr^{-1}, respectively. Similarly there was little difference in phosphorus and potassium litter production and decomposition between the three fertilizer treatments (Figures 5.15b and c, 5.16b and c and 5.17b and c). Since litter decomposition rates were the same for all fertilizer treatments, differences in nutrient release were a function of total litter production and litter pool size. The latter was not measured.

The nutrient released to the soil by decomposition represents 37, 20 and 18% of the nitrogen, phosphorus and potassium, respectively, in the total litter produced from shrubs fertilized with PAS. For shrubs fertilized with PU, this represents 35, 25 and 21%, respectively, and for unfertilized shrubs, 35, 25 and 15%, respectively. For each of the fertilizer treatments this is similar to nutrient return to the soil recorded for shrubs prior to the application of inorganic fertilizers (Section 3.5.3).

Nitrogen was the nutrient acquired in the largest quantities in the nutrient pool in both the above- and below-ground biomass. For shrubs fertilized with PAS, total plant uptake of nitrogen was 5 303 mol ha^{-1} yr^{-1} (Figure 5.15a). For shrubs receiving PU, despite higher levels of nitrogen fertilization, nitrogen uptake was lower at 2 196 mol ha^{-1} yr^{-1} (Figure 5.16a). In both cases of inorganic fertilizer application, nitrogen uptake was greater than for unfertilized shrubs (1 201 mol ha^{-1} yr^{-1}) (Figure 5.17a). The proportion of nitrogen distribution to the nutrient pool in the above-ground biomass was similar between shrubs fertilized with PAS (93%) and PU (83%) but higher than for unfertilized shrubs (72%) ie. in unfertilized shrubs a greater proportion of nitrogen was retained in the nutrient pool in the below-ground biomass (Figure 5.17a). This nitrogen retention in the nutrient pool in the below-ground biomass of unfertilized shrubs was greater than that for shrubs prior to the application of inorganic fertilizers (Section 3.5.3).

Despite equal levels of phosphorus in PAS and PU, shrubs receiving PAS absorbed 170 mol ha^{-1} yr^{-1} of phosphorus (Figure 5.15b) compared to 98 mol ha^{-1} yr^{-1} for shrubs receiving PU (Figure 5.16b). There was greater phosphorus uptake for both fertilizer types when compared to the phosphorus uptake of 51 mol ha^{-1} yr^{-1} of unfertilized shrubs (Figure 5.17b).

For fertilized and unfertilized shrubs, the distribution of phosphorus between the nutrient pools in the above- and below-ground biomass was similar viz. 96, 95 and 88% to the nutrient pool in the above-ground biomass in shrubs fertilized with PAS, PU, and unfertilized control shrubs, respectively. This was similar to shrubs prior to the application of inorganic fertilizers (Section 3.5.3).

Potassium was the nutrient acquired in the second largest quantity by shrubs grown under each of the three fertilizer treatments. Shrubs receiving inorganic fertilizers absorbed comparable amounts of potassium (889 and 863 mol ha^{-1} yr^{-1} for shrubs fertilized with PAS and PU, respectively) (Figures 5.15c and 5.16c). This uptake of potassium by fertilized shrubs was more than double the uptake of potassium (344 mol ha^{-1} yr^{-1}) by unfertilized shrubs (Figure 5.17c). For shrubs fertilized with PAS and PU, the percentage of potassium allocated to the nutrient pool in the above- and below-ground biomass was of the same order (96 and 4, and 97 and 3%, respectively) and similar to potassium allocation in shrubs prior to the application of inorganic fertilizers (96 and 4% to the nutrient pool in the above- and below-ground biomass, respectively) (Section 3.5.3). This is in comparison to unfertilized shrubs where there was a higher percentage distribution of potassium to the nutrient pool in the below-ground biomass (9%).

In shrubs fertilized with PAS, nitrogen and phosphorus pool sizes in the above-ground biomass both showed positive annual increments (Figures 5.15a and b). However, the annual increment in the potassium pool size in the above-ground biomass of these shrubs was negative (Figure 5.15c). In shrubs fertilized with PU and in unfertilized shrubs, the nitrogen, phosphorus and potassium pool sizes in the above-ground biomass all showed negative annual increments (Figures 5.16a, b and c, and 5.17a, b and c, respectively). In cases where annual increments were negative, losses of the nutrients from the nutrient pools in the above-ground biomass exceeded inputs. This was similar to that found in seven year old shrubs prior to the application of inorganic fertilizers (Section 3.5.3) and continued growth was probably at the expense of nutrients already absorbed. This would result in a decline in the nutrient content of shrubs and, with increases in biomass, also a decline in nutrient concentration.

Declines in nitrogen and phosphorus concentration in shrubs fertilized with PU and unfertilized shrubs were described in Section 5.4.1. In Chapter 3 it was suggested that these declines could be predicted. For example, a comparison of seven year old shrubs with ten year old unfertilized shrubs shows the following:

> in April 1986, shrubs were composed of 0.78 kg leaves (Figure 3.1). Leaf nitrogen concentration in May 1986 was 0.83 mmol kg^{-1} (Figure 3.15a). Therefore, the nitrogen content of leaves in May 1986 was 0.65 mmol shrub^{-1} (0.78 kg leaves x 0.83 mmol

> kg^{-1}). From the nitrogen nutrient budget for seven year old shrubs (Figure 3.19a), the annual increment in the nitrogen pool in the above-ground biomass was -184 mol ha^{-1} yr^{-1}. Therefore, over two years this would be an estimated decrease of 368 mol ha^{-1} yr^{-1} (= 0.368 mmol $shrub^{-1}$ at a planting density of 1 000 shrubs ha^{-1}). Therefore, after two years, the leaf nitrogen content should be 0.282 mmol $shrub^{-1}$ (0.65 mmol $shrub^{-1}$ - 0.368 mmol $shrub^{-1}$). The total dry mass of unfertilized shrubs in 1988 was 7.87 kg (Table 5.1) of which 23% (1.81 kg) was made up of leaf material (Table 5.2). Therefore, the leaf nitrogen content of 0.282 mmol $shrub^{-1}$ is contained in 1.81 kg leaves. This results in a leaf nitrogen concentration of 0.16 mmol kg^{-1} (0.282 mmol/1.81 kg). The leaf nitrogen concentration of unfertilized shrubs in March 1988 was 0.32 mmol kg^{-1} (Figure 5.8c). Although the predicted leaf nitrogen concentration is half that of the actual leaf nitrogen concentration measured, this example does illustrate that the growth of shrubs at the expense of previously absorbed nutrients and the resultant negative annual increments in nutrient pools were real phenomena. The estimate of leaf phosphorus concentration is one third of the actual leaf phosphorus concentration. Although leaf potassium estimates are not possible due to the high variation recorded in leaf potassium concentrations, an estimate of stem potassium concentration is approximately two thirds of the actual stem potassium concentration measured.

Annual increments in the nutrient pools in the below-ground biomass and the litter were positive for each of the three nutrients and for each of the three fertilizer treatments. Nitrogen increments were greater than for both potassium and phosphorus, respectively. The nitrogen increment in the nutrient pools in below-ground biomass and litter were greater for shrubs fertilized with PAS (368 and 288 mol ha^{-1} yr^{-1})

than for shrubs fertilized with PU (358 and 273 mol ha^{-1} yr^{-1}) and unfertilized shrubs (337 and 238 mol ha^{-1} yr^{-1}) (Figures 5.15a, 5.16a and 5.17a). However, it is likely that these differences are not significant. There was little variation in phosphorus and potassium increments in the nutrient pools between shrubs fertilized with PAS, PU or unfertilized shrubs (Figures 5.15b and c, 5.16b and c, and 5.17b and c).

5.5.4 **Summary**

Figures 5.18, 5.19 and 5.20 illustrate summarised annual nutrient budgets for shrubs fertilized with PAS, PU, and unfertilized control shrubs, respectively. The plant/soil system (P/SS) comprises the nutrient pools in the above- (AGB) and below-ground (BGB) biomass, available/soluble soil (AS) and total soil (TS) and the soil (S). Inputs were from rainfall (R) and inorganic fertilizers (F), and outputs are due to flower harvesting (FH) and stream-water (SW). Units for pool sizes are mol ha^{-1} and for nutrient flows, mol ha^{-1} yr^{-1}.

In both cases where shrubs received inorganic fertilizers there was an annual budget surplus for nitrogen, phosphorus and potassium (Figures 5.18 and 5.19). In contrast, for shrubs not fertilized there is an annual budget deficit for each of the three nutrients (Figure 5.20). This budget deficit is slightly larger than that recorded for shrubs prior to the application of inorganic fertilizers (Section 3.5.4). Of particular interest is the nitrogen surplus of 57 828 mol ha^{-1} yr^{-1} for shrubs fertilized with PU (Figure 5.19a). This is considerably greater than the surplus of 31 148 mol ha^{-1} yr^{-1} for shrubs fertilized with PAS. This is to be expected since urea contains more nitrogen than ammonium sulphate. However, the nitrogen content in the pools of the above- and below-ground biomass of PU shrubs (Figure 5.19a) is lower than that of the nitrogen content in the pools of the above- and below-ground

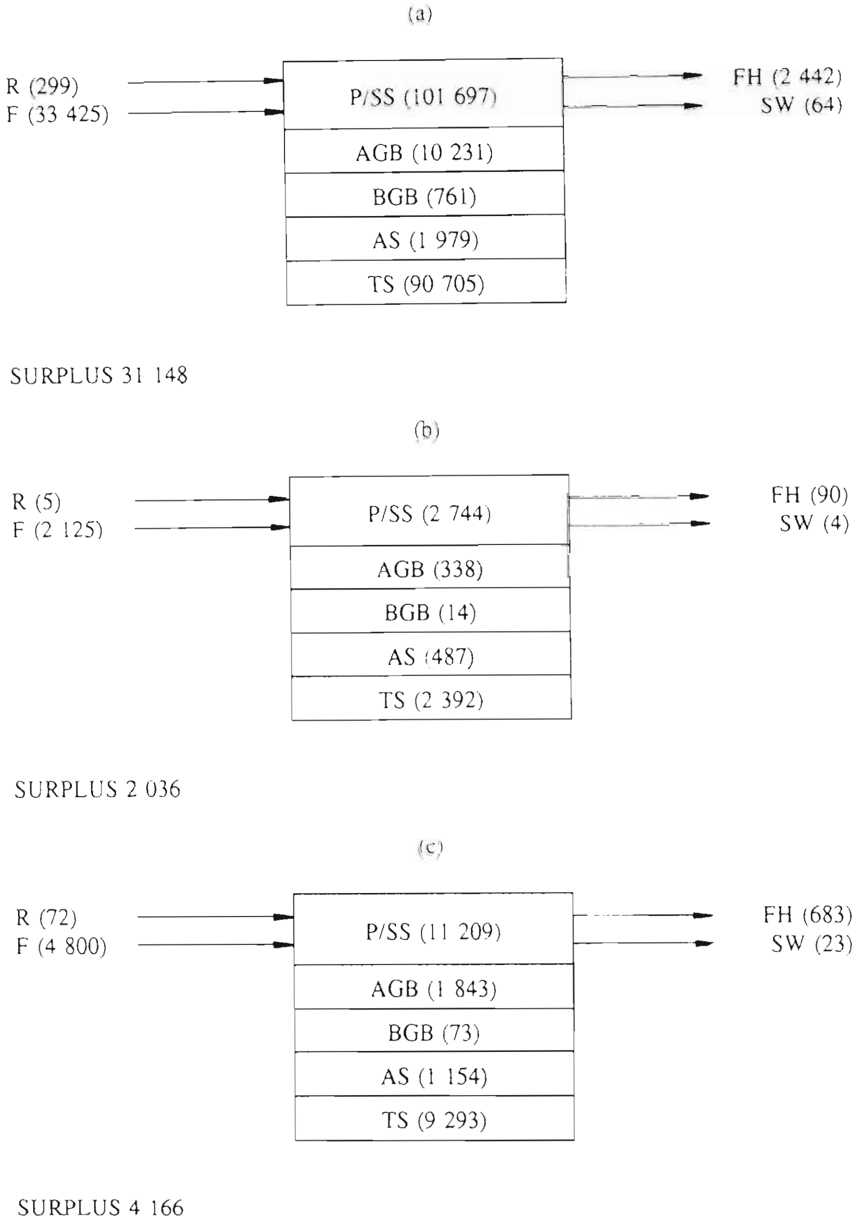


Figure 5.18 Summarised annual nutrient budgets (a) nitrogen, (b) phosphorus, and (c) potassium for *P. neriifolia* cultivated in a summer rainfall area with the application of the inorganic fertilizer Plantosan plus ammonium sulphate. The plant/soil system (P/SS) comprises the nutrient pools in the above- (AGB) and below- (BGB) ground biomass, available/soluble soil (AS), and total soil (TS). Inputs were from rainfall (R) and inorganic fertilizers (F), and outputs are due to flower harvesting (FH) and streamwater (SW).

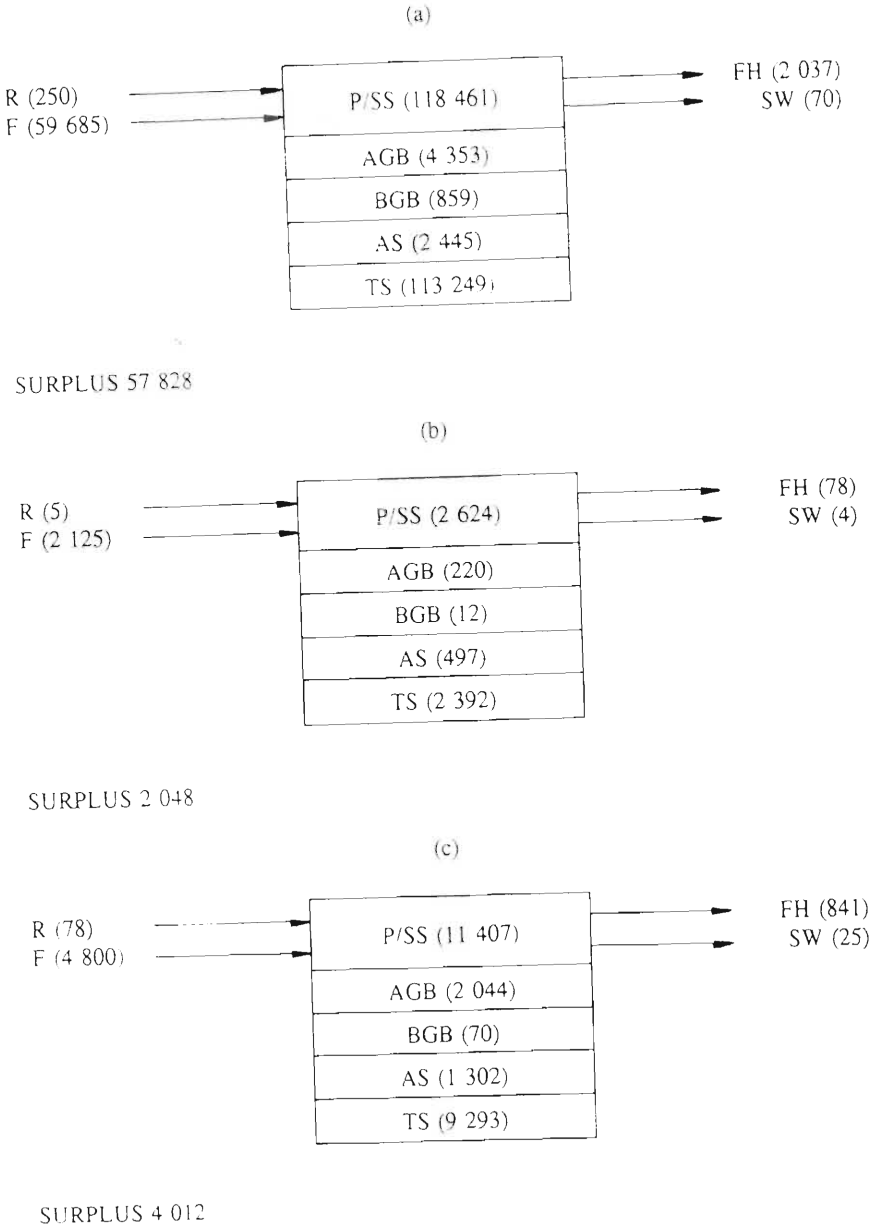


Figure 5.19 Summarised annual nutrient budgets (a) nitrogen, (b) phosphorus, and (c) potassium for *P. neriifolia* cultivated in a summer rainfall area with the application of the inorganic fertilizer Plantosan plus urea. The plant/soil system (P/SS) comprises the nutrient pools in the above- (AGB) and below- (BGB) ground biomass, available/soluble soil (AS), and total soil (TS). Inputs were from rainfall (R) and inorganic fertilizers (F), and outputs are due to flower harvesting (FH) and stream-water (SW).

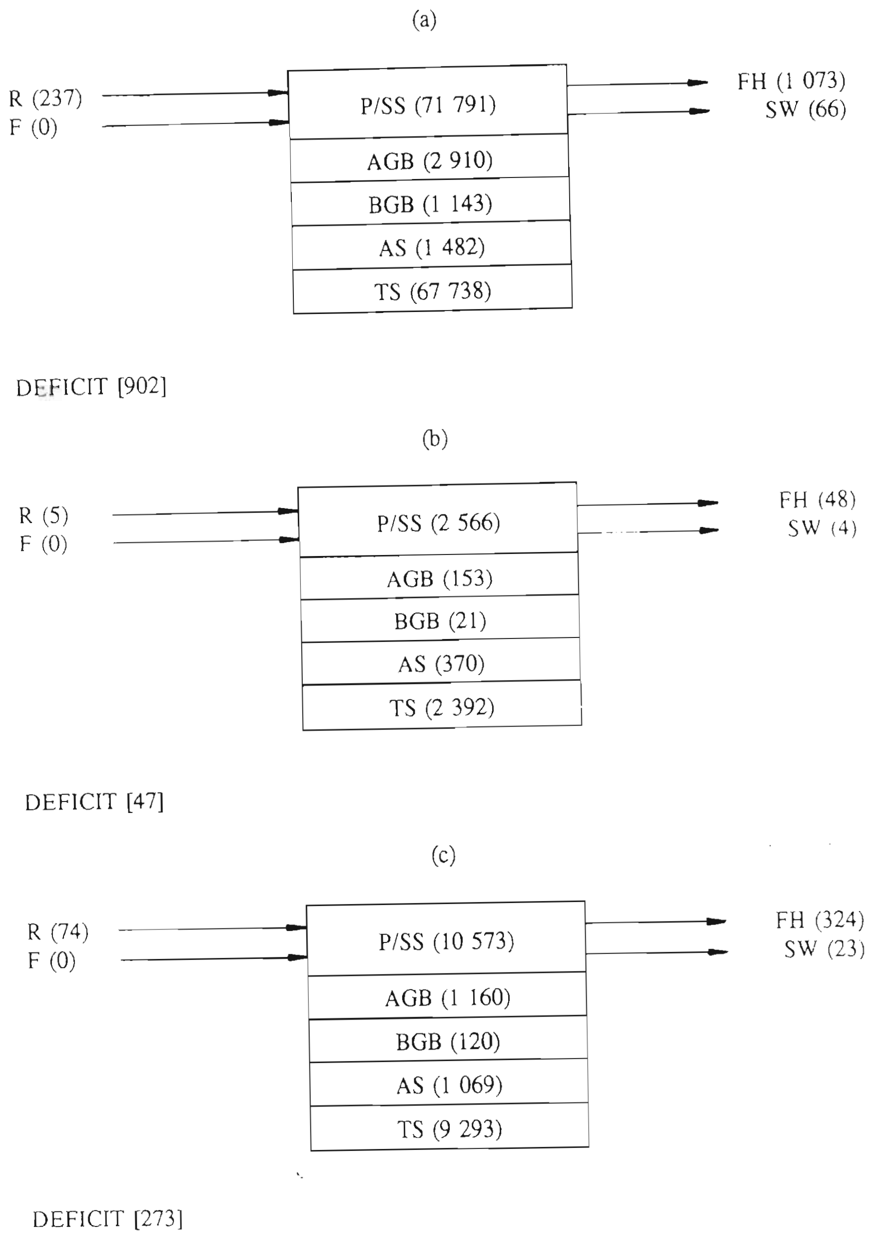


Figure 5.20 Summarised annual nutrient budgets (a) nitrogen, (b) phosphorus, and (c) potassium for *P. neriifolia* cultivated in a summer rainfall area without the application of inorganic fertilizers. The plant/soil system (P/SS) comprises the nutrient pools in the above- (AGB) and below- (BGB) ground biomass, available/soluble soil (AS), and total soil (TS). Inputs were from rainfall (R) and inorganic fertilizers (F), and outputs are due to flower harvesting (FH) and stream-water (SW).

biomass of PAS shrubs (Figure 5.18a). This suggests that nitrogen fertilizer saturation levels were attained with shrubs fertilized with PU, where despite increased levels of applied nitrogen there was no corresponding increase in shrub growth or shrub nitrogen concentration. It also suggests that nitrogen in the urea form is not as available to *P. neriifolia* as nitrogen in the ammonium form.

It is likely that for each of the fertilizers applied, nitrogen, phosphorus and potassium were applied in levels greater than that required to redress potential deficits, and at rates greater than required for shrub growth. This would account for the high surpluses calculated for each of the nutrients without correspondingly high increases in nutrient pools in the above- and below-ground biomass. The lack of a corresponding increase in the nutrient pools in the above- and below-ground biomass and the total soil for all three nutrients in fertilized systems could reflect excess fertilization. Although soil soluble and total nitrogen and available phosphorus did increase slightly as a result of inorganic fertilization (Table 5.8), increases did not reflect the large surpluses recorded in the budget summaries. This suggests the loss of the bulk of the nutrients from the soil system, probably via runoff. Runoff and soil leaching were, however, not measured and, although stream-water samples were taken approximately 15 months after initial fertilizer applications, it is unlikely that the fertilizer surpluses could be measured in stream-water. This is because the protea orchard contributed only 10% of the catchment to total stream-flow (Section 2.4.3). Also, as mentioned earlier, fertilizer application rates refer only to the protea component and not the entire plant community within the one hectare, the area on which the budgets are calculated. Therefore, the concentration of the excess nutrients would be diluted when sampled in stream-water. It is probable, therefore, that the large nitrogen, phosphorus and potassium surpluses illustrated in Figures 5.18 and

5.19 are lost to the entire system, and no longer form part of the nutrient budgets of the cultivated shrubs.

That some form of nutrient addition is required is illustrated clearly by those shrubs not fertilized. As with shrubs prior to the addition of fertilizers, there was a deficit for each of the nutrients, particularly as a result of the harvesting of flowers for commercial sale. This is further reflected by the reduced growth recorded for these shrubs (Sections 5.1 and 5.2).

During the entire study, measurements were made on shrubs from which flowers were removed, simulating the harvest of flowers for commercial sale. Therefore, there are no budgets reflecting the growth and nutrient cycling of cultivated *P. neriifolia* in the absence of flower harvesting. This is because it was felt that the flower harvest component of any budget can be added to the nutrient pool in the above-ground biomass to reflect such a scenario. It is interesting to note, therefore, that in the absence of flower harvesting there would be an accumulation of nitrogen, phosphorus and potassium in the nutrient pools of the above-ground biomass for shrubs of all fertilizer treatments, including those shrubs not fertilized (Figures 5.15, 5.16 and 5.17). As with shrubs prior to the application of inorganic fertilizers (Section 3.5.4), this accumulation reflects the efficient internal cycling of nitrogen, phosphorus and potassium within the plant/soil system.

6 DISCUSSION

The present study was undertaken to quantify the growth and mineral cycling of *P. neriifolia* in a cultivated orchard, particularly in the light of nutrient depletion through the removal of flowers for commercial sale.

This was achieved by monitoring the growth, phenology and nutrient cycling in a cultivated *P. neriifolia* orchard (Chapter 3), assessing the effect of ammonium nitrogen, phosphorus and potassium on the growth of *P.neriifolia* seedlings (Chapter 4) to serve as a base for inorganic fertilizer applications in established *P. neriifolia* orchards, and monitoring the effects of inorganic fertilizers on the growth, phenology and nutrient cycling in an established *P. neriifolia* orchard (Chapter 5).

Data will be interpreted with reference to existing information on the growth and mineral cycling of the Proteaceae and other mediterranean ecosystem plants growing in their natural habitat, and with reference to available literature on the nutrition of container- and/or field-grown Proteaceae.

This discussion will deal with the following: a comparison of the climate and soils of MSNR and mediterranean ecosystems; an analysis of *P. neriifolia* seedling responses to applied nitrogen, phosphorus and potassium; and an evaluation of the influence of shrub age and applied nutrients on the growth, phenology and nutrient cycling of cultivated *P. neriifolia* prior to and after the application of inorganic fertilizers. A brief summary of horticultural implications arising from this study is also presented.

6.1 Climate and soils

Since the natural distribution of the Proteaceae is in the mediterranean ecosystems of the south-western Cape of South Africa (Goldblatt, 1978; Taylor, 1978; Kruger, 1979) and south-western and south-eastern Australia (Specht, 1979), areas characterised by winter rainfall (Day, 1983), the major climatic difference between the Mount Sheba Nature Reserve (MSNR) cultivation site and the natural distribution areas of the Proteaceae is the summer rainfall at MSNR (Figures 2.4 and 2.5).

With regard to other climatic features, the climate of MSNR closely matches that of mediterranean ecosystems. As with mediterranean ecosystems (Day, 1983), seasons at MSNR are well-defined with cool winters and warm summers (Figures 2.4 and 2.5). Winter and summer minimum and maximum temperatures equal to 9.0 and 19.7° C, and 12.2 and 22.0° C, respectively, fall within the range described for mediterranean ecosystems (Day, 1983). Furthermore, frost and snow occurrences are similar to that described by Day (1983) (Section 2.1.2).

The soils of MSNR, unamended by inorganic fertilizer applications, are well drained, highly leached, and of low nutrient status (Table 2.1) . Using data and criteria proposed for mediterranean ecosystems (Table 2.2), the nutrient poor soils of MSNR are comparable to strongly leached heathland soils.

Therefore, the abiotic components of the MSNR cultivation site studied in this investigation closely match the abiotic characteristics described for the natural distribution regions of the Proteaceae. The single most significant difference is the summer rainfall pattern at MSNR compared to the winter rainfall pattern in mediterranean ecosystems. The importance of this difference in rainfall patterns depends on whether *P. neriifolia* is normally water or nutrient limited. Although water relations of *P. neriifolia* were not studied, neither seedlings nor sprouters of *P. nitida*, growing in their natural habitat of the south-western Cape of South Africa, showed signs of severe drought in a mediterranean-climate context (Smith, 1990). Therefore, although *P. neriifolia* cultivated at MSNR experienced summer rainfall, the timing of rainfall may be less important than the availability of nutrients.

6.2 The response of *P. neriifolia* seedlings to added nutrients

Information on the nutritional requirements of the Proteaceae is both limited and poorly defined (Parvin, Criley and Bullock, 1973; Groves and Keraitis, 1976;

Thomas, 1979; 1980; 1981; Tibbits and Bachelard, 1981; Vogts, 1982) and of a generalised nature, for example, the nutrient requirements are low (Claassens, 1981; Stock and Lewis, 1982; Vogts, 1982; Heinsohn and Pammenter, 1986; Parvin, 1986). This has resulted from the observation that in their natural habitat Proteaceae grow on well drained soils of low mineral content (Vogts, 1958; Jeffrey, 1964; Moore, 1966; Hocking and Thomas, 1974; Vogts, 1977a,b; Vogts, 1982).

Furthermore, available information appears confused and this can be attributed to three possible causes : (a) studies have been performed on individual species and results are, therefore, only of intraspecific significance, (b) studies on species' specific nutritional characteristics have been incorrectly extrapolated to be representative of all members of the Proteaceae, and (c) toxicity effects have been studied in preference to nutritional requirements.

6.2.1 Growth responses

As in some past work on the nutrient requirements of Proteaceae (Claassens and Foelscher, 1980), in this investigation the primary response of *P. neriifolia* seedlings was increased growth with increased levels of applied ammonium nitrogen, to a maximum ammonium nitrogen level between 4 and 7 mM (= 56 and 98 ppm N) (Section 4.1). Unlike in the case of *P. repens* seedlings (Witkowski, 1989b), this response was seen in total stem length, and shoot, root and total dry mass of the seedlings. It is likely, therefore, that *P. neriifolia* has a higher nitrogen demand than the low demand reported for *P. repens* (Stock and Lewis, 1984). At ammonium nitrogen levels higher than 7 mM viz. 10 mM (= 140 ppm N), growth was reduced. This response to nitrogen is similar to that recorded for a number of species of the Proteaceae (Van Staden, 1968; Nichols and Beardsell, 1981; Thomas, 1982; Heinsohn, 1983; Heinsohn and Pammenter, 1986). Similarly, in *P. cynaroides* nitrogen deficiency had the most profound effect on the general growth of the plants (Van Staden, 1967). In contrast, however, Lewis and Stock (1978) found poor utilisation of additional nitrogen (14.3 ppm N) by *Leucadendron xanthoconus* shoots.

Phosphorus and potassium did not appear to affect the growth of *P. neriifolia* seedlings at the lowest (1 mM N (= 14 ppm N)) or highest (10 mM N) level of ammonium nitrogen application (Section 4.1). At moderate (4 mM N) to relatively high (7 mM N) levels of ammonium nitrogen application, there was increased growth with increasing levels of applied phosphorus and potassium, to maximum growth at the highest level of application of these two nutrients (0.65 mM P (= 20.1 ppm P) and 1.25 mM K (= 48.9 ppm K), respectively). This effect of phosphorus is similar to that recorded in *Grevillea* cv. Poorinda Firebird (Nichols and Beardsell, 1981) although phosphorus toxicity was recorded in the *Grevillea* seedlings at phosphorus levels double that applied in this investigation. These toxicity effects at phosphorus levels of 1.28 mM P (= 39.6 ppm P) were, however, alleviated by high nitrogen (8 mM (= 112 ppm N) and high potassium (2.56 mM (= 100 ppm K)) levels (Nichols and Beardsell, 1981). Optimum growth of the *Grevillea* seedlings was recorded at phosphorus levels of 0.16 mM (= 5 ppm P) (Nichols and Beardsell, 1981) and this is considerably lower than the maximum 0.65 mM P (= 20.1 ppm P) tested in this investigation. Similarly, the phosphorus concentration resulting in optimum growth in this investigation is considerably higher than the 'safe upper limit' of 15 ppm P (Nichols, 1981) or the 6 ppm P (Thomas, 1982) suggested for a wide range of members of the Family Proteaceae.

Grundon (1972) and Nichols and Beardsell (1981) suggest that in *Grevillea* cv. Poorinda Firebird, growth responses due to nitrogen and potassium were dependent on phosphorus levels, and that the increases in growth which occurred at high levels was due to the alleviation of phosphorus toxicity. Similarly, in *P. repens* seedlings, total dry mass increased with increasing applications of phosphorus, whereas nitrogen applications resulted in reduced total dry mass (Witkowski, 1989b). In the investigation reported here, however, it was found that the growth effects due to phosphorus and potassium were dependent on the ammonium nitrogen concentration, and that phosphorus and potassium effects were apparent only at moderate to relatively high ammonium nitrogen concentrations.

In contrast to this investigation, Groves and Keraitis (1976) recorded death of *Banksia serrata* seedlings at nitrogen and phosphorus levels comparable to those studied in this investigation. It is likely, therefore, that Proteaceae vary in their sensitivity to various nutrients, particularly nitrogen and phosphorus. This is supported by growth response data for *Leucospermum cordifolium* which appeared more tolerant of varying nitrogen, phosphorus and potassium levels than did a *Protea longiflora* x *P. lacticolor* hybrid known as Ivy (Claassens and Foelscher, 1980).

Similarly, *Hakea laurina* exhibited tolerance to phosphorus at phosphorus levels of 36 ppm (Thomas, 1982). Nichols (1981) evaluated sensitivity to phosphorus toxicity of 33 members of the Proteaceae and suggested the possibility of genetic variation in tolerance to phosphorus. Nichols and Beardsell (1979) suggested a low phosphorus sensitivity in the *Grevillea* species and a high phosphorus sensitivity in the *Protea* and *Leucadendron* species. However, Prasad and Dennis (1986) reported no toxicity effects in *Leucadendron salignum* cv. Safari Sunset grown under conditions of high soil phosphorus (40 ppm) availability. In general, therefore, the statement that all members of the Proteaceae are sensitive to high levels of phosphorus in the growing medium (Knauer, 1987) requires qualification and quantification.

There exists little information on the potassium nutrition of the Proteaceae. However, *Grevillea* cv. Poorinda Firebird has been grown successfully at potassium concentrations of 0.64 mM (= 25 ppm K) and 2.56 mM (= 100 ppm K) (Nichols and Beardsell, 1981). In the current investigation, optimum *P. neriifolia* seedling growth was at 1.25 mM K (= 48.9 ppm K) at moderate to relatively high ammonium nitrogen concentrations. Similarly, *Grevillea* response to potassium at higher levels was also associated with increased nitrogen availability (Nichols and Beardsell, 1981).

Potassium is an element of importance in many physiological processes, for example, osmoregulation and stomatal movements (Clarkson and Hanson, 1980). The potassium levels tested for the growth of Proteaceae are lower than those utilized by other plants (Clarkson and Hanson, 1980; Thomas, 1982) and this is in contrast to the physiological importance of potassium, particularly since high potassium levels have been reported to be toxic to the Proteaceae (Claassens, 1981).

Low shoot/root dry mass ratios are generally indicative of plants from nutrient poor habitats (Loneragan and Asher, 1967; Biddiscombe, Ozanne, Barrow and Keay, 1969; White, 1972; Brewster, Bhat and Nye, 1975; Christie and Moorby, 1975). In this investigation, shoot/root ratios were low (< 1), particularly when compared to shoot/root dry mass ratios for two year old pot-grown *Leucadendron floridum* (4.8), *Leucospermum formosum* (5), and *Leucospermum oleifolum* (6.2) (Lamont, 1983b). However, the *P. neriifolia* seedlings in the current investigation were harvested after one year and it is likely that shoot/root ratios will increase with age of the plants. Seedlings of *P. repens* exhibited increasing shoot/root dry mass ratios with increasing applications of nitrogen and phosphorus (Witkowski, 1989b). However, as with *P. repens* (Witkowski, 1979b), *P. neriifolia* is a slow growing species and possibly does not exhibit much phenotypic plasticity in shoot/root ratio (especially at the seedling stage), particularly in comparison to faster growing plants (Chapin, 1980).

6.2.2 Seedling nutrient concentrations

The concentration of nitrogen in the above-ground plant tissue varied from 0.32 to 1.22 mmol g^{-1} (Table 4.7). Highest tissue nitrogen concentration was measured in seedlings receiving the highest concentration of applied ammonium nitrogen (10 mM). However, due to the reduced growth of seedlings at 10 mM N, the nitrogen content of these seedlings was lower than that for seedlings receiving 4 and 7 mM ammonium nitrogen (Section 4.2).

The above-ground plant tissue nitrogen concentrations at optimum ammonium nitrogen supply for these seedlings were higher than the nitrogen concentration in leaves of wild populations of *P. repens* (0.39 mmol g^{-1}), *P. compacta* (0.36 mmol g^{-1}), *P. neriifolia* (0.39 mmol g^{-1}) and *Banksia hookeriana* (0.47 mmol g^{-1}) (Low and Lamont, 1986) and nursery fed *Hakea laurina* (0.50 mmol g^{-1}) (Thomas, 1982). However, nitrogen levels were similar to those recorded for a range of other members of the Family Proteaceae, for example, nitrogen concentrations of green leaves of field cultivated *Banksia ornata* (0.87 mmol g^{-1}), *P. neriifolia* (0.71 mmol g^{-1}), *P. cynaroides* (0.69 mmol g^{-1}), *P. eximia* (0.91 mmol g^{-1}) and *Leucospermum cordifolium* (0.85 mmol g^{-1}) (Parvin, 1986). Plant nitrogen levels in this investigation were, however, also approximately 50% lower than those recorded for hydroponically grown *Leucadendron salignum* (Heinsohn, 1983), wild populations of *Leucadendron xanthoconus*, *P. lepidocarpodendron* and *P. laurifolia* (Lewis and Stock, 1978), and lower than nitrogen concentrations recorded in nursery fed *Grevillea* cv. Poorinda Firebird (1.27 mmol g^{-1}) (Nichols and Beardsell, 1981) and nursery fed *P. cynaroides* (1.31 mmol g^{-1}) (Van Staden, 1968). There is, therefore, wide variation in plant nitrogen levels and it is likely that genetic variation as well as environmental factors influence nitrogen absorption and utilization.

Furthermore, all levels of tissue nitrogen recorded for the Proteaceae are lower than in non-proteaceous plants. For example, Lewis and Stock (1978) recorded that the nitrogen concentration in *Datura stramonium*, grown in fertilized agricultural soil, was 12 times greater than that of four naturally occurring, mature species of Proteaceae. Similarly, the tissue nitrogen concentration of *D. stramonium* was 12 times greater than that recorded for *P. neriifolia* seedlings in the current investigation, despite the growth of the *P. neriifolia* seedlings under conditions of high ammonium nitrogen supply.

The phosphorus (range = 0.016 to 0.027 mmol g^{-1}; mean = 0.02 ± 0.002 mmol g^{-1}) and potassium (range = 0.17 to 0.27 mmol g^{-1}; mean = 0.23 ± 0.02 mmol g^{-1}) concentration of *P. neriifolia* seedlings did not vary much at the different levels of applied ammonium sulphate, phosphorus or potassium (Tables 4.8 and 4.9). This suggests absorption and utilization of only as much phosphorus and potassium as required for growth. However, there were differences in seedling phosphorus and potassium levels in comparison with levels recorded for other wild and nursery fed proteaceous shrubs. Seedling phosphorus levels in this investigation were higher than those recorded for wild populations of *P. repens, P. compacta, P. neriifolia* and *B. hookeriana* (Low and Lamont, 1986), similar to those recorded for field cultivated *B. ornata, Leucospermum cordifolium, P. neriifolia, P. cynaroides* and *P. eximia* (Parvin, 1986), and lower than those recorded for nursery fed *Grevillea* cv. Poorinda Firebird (Nichols and Beardsell, 1981) and nursery fed *P. cynaroides* (Van Staden, 1968). Plant potassium levels recorded in this investigation were higher than those recorded in a range of wild (Low and Lamont, 1986) and cultivated (Parvin, 1986) species, and nursery fed *H. laurina* (Thomas, 1982), similar to nursery fed *Grevillea* cv. Poorinda Firebird (Nichols and Beardsell, 1981), *Banksia ornata* (Jeffrey, 1964; 1967) and *Hakea obliqua* (Dell, Kuo and Thompson, 1980), and lower than in nursery fed *P. cynaroides* (Van Staden, 1968). As with plant nitrogen concentrations, phosphorus and potassium concentrations in the Proteaceae are lower than levels of the same nutrients in non-proteaceous plant life forms (Rorison, 1968; Woodhouse, Wild and Clement, 1978; Fife and Nambiar, 1984; Pastor, Aber, McClaugherty and Melillo, 1984).

Unlike in *P. repens*, where seedling phosphorus levels increased with increasing supply of phosphorus and decreased with increasing supply of nitrogen (Witkowski, 1989b), *P. neriifolia* seedlings exhibited increased nitrogen concentration with increased ammonium nitrogen supply, and no significant differences in seedling phosphorus and potassium concentrations at all levels of phosphorus and potassium supply (Section 4.2). Therefore, as shown by multifactor analysis of variance (Table 4.10), interactive effects of applied nutrients on seedling nitrogen, phosphorus and potassium levels were not as pronounced in *P. neriifolia* as recorded for *P. repens* (Witkowski, 1989b).

It is interesting to note *P. neriifolia* seedling nitrogen, phosphorus and potassium concentrations (Tables 4.7, 4.8 and 4.9) were similar to leaf nutrient concentrations recorded in seven year old *P. neriifolia* shrubs prior to the application of inorganic fertilizers (Figures 3.15a, 3.16a and 3.17a), and ten year old shrubs after the application of Plantosan plus ammonium sulphate (Figures 5.8a, 5.10a and 5.12a). Seedling nutrient concentrations at optimum levels of nutrient supply were, however, greater than leaf nutrient concentrations in ten year old shrubs fertilized with Plantosan plus urea and ten year old unfertilized shrubs (Figures 5.8b and c, 5.10b and c, and 5.12b and c).

6.2.3 Summary

The wide variation in plant nutrient concentrations highlights the difficulty in working with wild as opposed to highly bred flora, and also the differences that may occur between seedlings (juvenile) and mature shrubs. Further, it highlights the necessity of recording species and variant specific responses to specific forms of nutrients without extrapolating results to be representative of all the Proteaceae. For example, in this investigation the source of nitrogen was ammonium sulphate (ie. ammonium nitrogen only). In the case of similar work conducted with *P. repens,* the source of nitrogen was ammonium nitrate, a mixture of ammonium and nitrate nitrogen (Witkowski, 1989b). Therefore, the increase in plant growth of *P. neriifolia* seedlings to increasing ammonium nitrogen supply, which was in direct contrast to a reduction in *P. repens* growth with increasing ammonium nitrate supply (Witkowski, 1989b), could be explained partly by the different forms of nitrogen applied to the respective plants. This is particularly important as certain species of Proteaceae have been shown to be sensitive to high levels of nitrate nitrogen (Claassens, 1981; Nichols and Beardsell, 1981; Vogts, 1982; Heinsohn, 1983). Finally, the wide variation in plant nutrient concentrations obtained in seedlings supplied with different levels of nutrients precludes the possibility of calculating critical nutrient concentrations (Bates, 1971) for the Proteaceae.

The primary aim of the nursery trial in which *P. neriifolia* seedlings were grown for one year under different combinations of varying levels of ammonium nitrogen, phosphorus and potassium was to determine an NPK combination that resulted in optimum seedling growth and which could be applied to field cultivated shrubs. The determination of this NPK balance of nutrient resources is important because although plants can compensate for imbalances (Chapin, Bloom, Field and Waring, 1987), an increase in the availability of one nutrient only may result in a decrease in the relative availability of other nutrients (Lajtha and Klein, 1988).

Optimum growth was recorded at an NPK ratio of 4.5:1:2.5 (mass basis) and the best fit to a commercial fertilizer was to Plantosan (Section 4.3). However, for reasons detailed in Section 4.3, it was decided to supplement Plantosan with additional nitrogen. Ammonium sulphate and urea were used separately as nitrogen supplements. In the case of ammonium sulphate, no detrimental effect was anticipated due to increased sulphate (Moore, 1966). Furthermore, the choice of a slow release fertilizer was in accordance with recommendations for the field fertilization of Proteaceae (Dixon, 1980; Elliot and Jones, 1980; Worrall, 1983).

6.3 The growth and phenology of *Protea neriifolia* cultivated in a summer rainfall area

6.3.1 Growth

Whole shrub dimensions

Data on whole shrub dimensions for the Proteaceae are limited and, due to the wide variety of species and growth forms, highly variable (Rourke, 1980; Vogts, 1982). Average shrub dimensions of six year old *P. neriifolia* are 1.25 to 1.5 m in height, and almost as broad as high (Vogts, 1977a). The average diameter of the main stem of five year old *P. neriifolia* is 6 cm (Vogts, 1977a). These data compare favourably to shrub dimension data for seven year old cultivated *P. neriifolia* (Table 3.1). Furthermore, increases in shrub dimensions with age have been recorded, for example, the average shrub height of 15 year old *P. neriifolia* has been recorded as between 2.5 and 3 m (Vogts, 1977a) or 2.67 to 3.33 m (Werner, 1951), while the stem diameter increases with age and can be as high as 22 cm in 12 year old *P. neriifolia* (Vogts, 1977a). The height of cultivated *P. neriifolia* shrubs did increase with age and as a result of the application of inorganic fertilizers, and in 10 year old cultivated shrubs ranged from 2.57 to 3.12 m (Table 5.1), comparable to the average described by Vogts (1977a). Stem diameters of cultivated shrubs also increased with age and as a result of the application of inorganic fertilizers (Tables 3.1 and 5.1) but did not reach 22 cm as described by Vogts (1977a).

Canopy dimensions, for example, dimensions along and across the line, and canopy radius, did not vary much with increasing shrub age or the application of inorganic fertilizers (Tables 3.1 and 5.1). This is thought to be as a result of the harvesting of flowers for commercial sale. However, dimensions along and across the line were comparable with a shrub diameter of 2 m, as described by Rourke (1980).

In order to facilitate comparisons with other work on the Proteaceae, data from this investigation have been converted to allow expression as g m^{-2}. It is important to note that, as with the data cited (which refer to the proteaceous component of a community only), data from the current study refer to the protea component of the cultivated orchard only. The total (above- and below-ground) biomass of cultivated but unfertilized *P. neriifolia* shrubs increased from 1 085 g m^{-2} for a seven year old shrub to 2 997 g m^{-2} for a ten year old shrub (Tables 3.1 and 5.1). In comparison, the total biomass of ten year old shrubs fertilized with Plantosan plus ammonium sulphate and Plantosan plus urea was 4 669 and 3 708 g m^{-2}, respectively (Table 5.1). Low and Lamont (1986) have recorded an above-ground biomass of 3 240 g m^{-2} for 21 year old *P. neriifolia* shrubs and an above-ground biomass of 6 817 g m^{-2} for 11 year old *P. repens*. Similarly, Van Wilgen (1982) has recorded an above-ground biomass of 930 and 2 310 g m^{-2} for *P. neriifolia* and *P. repens*, respectively, 21 years since the last fire. From this data it is evident that *P. repens* is a faster growing proteaceous shrub than *P. neriifolia*, and unfertilized and fertilized *P. neriifolia* cultivated in a summer rainfall area are faster growing than plants occurring in their natural habitat at Jonkershoek, Cape Province, South Africa, an area described as being more productive than other mediterranean-type ecosystems (Van Wilgen, 1982). The better growth of *P. neriifolia* cultivated in a summer rainfall area is further highlighted when compared with above-ground biomass data for heathland communities of similar age, for example, 11 year old coastal fynbos (1 458 g m^{-2}) (Low, 1983), 12 year old mountain fynbos (558 g m^{-2}) (Van Wilgen and le Maitre, 1981), 15 year old Australian heath (1 111 g m^{-2}) (Specht, Rayson and Jackman, 1958).

There was no significant difference in the canopy area of cultivated *P. neriifolia* shrubs, either as a result of increasing shrub age or as a result of the application of inorganic fertilizers (Tables 3.1 & 5.1). There was, however, an increase in canopy volume, both with increasing age of the shrubs and as a result of inorganic fertilizer applications. This is a response to increasing height of the shrubs (Section 5.1). The relatively constant canopy area of *P. neriifolia* is similar to that found for unfertilized and fertilized *Leucospermum parile* (Witkowski, Mitchell and Stock, 1990a). However, unlike *P. neriifolia* which did exhibit significant differences in canopy volume, *L. parile* canopy volume was of the same order for unfertilized and fertilized shrubs (Witkowski *et al.*, 1990a).

Total biomass and allocation patterns

The sequential increase in total biomass from 1986 to 1989 for *P. neriifolia* cultivated in a summer rainfall area was 1 085 (1986), 1 836 (1987), 2 110 (1988) and 2 997 (1989) g m^{-2} for unfertilized shrubs, 1 085 (1986), 1 836 (1987), 2 417 (1988) and 4 669 (1989) g m^{-2} for shrubs fertilized with Plantosan plus ammonium sulphate, and 1 085 (1986), 1 836 (1987), 2 145 (1988) and 3 708 (1989) g m^{-2} for shrubs fertilized with Plantosan plus urea (Table 5.1). The 1987 and 1988 data are derived from two different allometric relationships between stem diameter and plant dry mass (a and b, respectively; Section 2.2.1.1). For unfertilized *P. neriifolia* shrubs, total biomass increased by 41% between 1986 and 1987, 13% between 1987 and 1988, and 30% between 1988 and 1989. For shrubs fertilized with Plantosan plus ammonium sulphate, total biomass increased by 41% between 1986 and 1987 (prior to fertilization), 24% between 1987 and 1988 (first year of fertilization), and 48% between 1988 and 1989 (second year of fertilization). For shrubs fertilized with Plantosan plus urea these increases were 41% between 1986 and 1987 (prior to fertilization), 14% between 1987 and 1988 (first year of fertilization), and 42% between 1988 and 1989 (second year of fertilization). The lower total biomass increase between 1987 and 1988 for each fertilizer treatment is probably as a result of an underestimate of shrub dry mass using the two stem diameter/shrub dry mass allometric relationships. Since 1989 data are actual measurements, the positive influence of Plantosan plus ammonium sulphate and Plantosan plus urea on total biomass compared to unfertilized shrubs are significant. Also significant is that effects of fertilizers become apparent only two years after initial application. While herbaceous plants are more plastic and rapid in their morphological growth responses to inorganic fertilizers (Witkowski and Mitchell, 1989), evergreen shrubs (for example, *P. neriifolia* (this study) and *Leucospermum parile* (Witkowski, 1989c)) are less plastic and slower, and possibly more resilient to nutrient disturbances of this nature (Witkowski, 1989c; Witkowski and Mitchell, 1989). However, morphological growth responses in the second year of inorganic fertilizer applications do show that, unlike in *Leucospermum parile* (Witkowski and Mitchell, 1989), *P. neriifolia* does respond positively to increased levels of available soil nutrients. However, rapid growth responses to added nutrients may have implications for the longevity of the shrubs, since inorganic fertilizer applications can result in an accelerated life cycle culminating in early shrub death (Thomas, 1982).

The relative contribution of shrub components to total shrub dry mass (Figures 3.1 and 5.1) of cultivated *P. neriifolia* did change with increasing age of the shrubs and with the application of inorganic fertilizers. In all cases the over-riding contribution was that of stems, from 57 - 68% of total plant dry mass (Table 5.2). The most significant change in relative contributions of component dry mass to total dry mass occurred in the roots. Compared with unfertilized seven year old shrubs, ten year old shrubs fertilized with Plantosan plus ammonium sulphate showed a reduction in the proportion of non-proteoid roots. This proportion remained constant in ten year old shrubs fertilized with Plantosan plus urea and, in contrast, ten year old shrubs not fertilized showed a doubling in the proportion of non-proteoid roots (Table 5.2). Similar increases in the proportion of root material as a result of nutrient poor soils have been measured in plants in mediterranean ecosystems (Kummerow, Alexander, Neel and Fishbeck, 1978) and are thought to occur to allow more effective nutrient uptake from the nutrient poor soils (Mooney, Kummerow, Moll, Orshan, Rutherford and Sommerville, 1983). Since available soil levels of unfertilized shrubs were showing signs of depletion when compared with available soil levels of fertilized shrubs (Table 5.8), it is possible that low available soil levels for unfertilized shrubs were responsible for the increase in the proportion of non-proteoid roots in these shrubs. Conversely, the relative 'richness' of soils for fertilized shrubs resulted in the proportion of non-proteoid roots either decreasing (PAS) or remaining constant (PU). It is surprising, however, that changes in the proportion of proteoid roots, with age or fertilizer treatment, were not marked. This is because proteoid roots are responsible for the absorption of water and minerals, and are thought to be produced in response to low levels of available nitrogen and phosphorus in the soil (Lamont, 1986). Despite the relatively low phenotypic plasticity suggested for *P. neriifolia* seedlings earlier, due to the importance of proteoid roots in water and mineral absorption from soils of low nutrient availability, one would expect the most rapid changes in shrub dry mass composition in the proteoid root component.

The changes in the relative contribution of shrub components to shrub total dry mass described above resulted in comparable changes in shoot/root dry mass ratios ie. an increase in the shoot/root ratio of shrubs receiving inorganic fertilizers compared with a decrease in unfertilized shrubs (Table 5.3).

There exist no comparative data on the relative contributions of components to total shrub dry mass for the Proteaceae. However, comparisons can be drawn with other plants. For example, the composition of total plant dry mass of pine growing in mediterranean-climate regions in France is: shoot and wood (89.7%), leaves (3.8%) and roots (6.5%) (Cabanettes, 1979 loc. cit. Ehleringer and Mooney, 1983), and that of chaparral shrub in California: shoot and wood (70%), leaves (6.9%), and roots (23.1%) (Kittredge, 1955; Specht, 1969, and Kummerow, Krause and Jon, 1977 loc. cit. Ehleringer and Mooney, 1983). In each case stems (shoot and wood) contribute significantly more than other plant parts to total dry mass. Unlike in *P. neriifolia*, in the above two examples, leaves contribute less than the roots to total dry mass. The contribution of below-ground biomass to total biomass of 30 month old *P. nitida* seedlings occurring in their natural habitat was more than double that of above-ground biomass (Smith, 1990). Similarly, in 15 year old south-eastern Australian heath, the distribution between above- and below-ground biomass is 15 and 85%, respectively (Specht *et al.*, 1958). In contrast, however, in 11 year old coastal fynbos, the distribution between above- and below-ground biomass is 51 and 49%, respectively (Low, 1983). Wide variations in the relative contribution of above- and below-ground biomass to total biomass were also reported for a range of Chilean matorral plants (Hoffman and Kummerow, 1978).

Leaf/stem dry mass ratios also showed significant differences with time and between fertilizer treatments (Section 3.1 and Table 5.3). In shrubs fertilized with Plantosan plus ammonium sulphate the leaf/stem dry mass ratio remained constant with increasing shrub age indicating no change in allocation patterns in these shrubs. However, for unfertilized shrubs and shrubs fertilized with Plantosan plus urea, there was a significant increase in leaf/stem dry mass ratio with increasing shrub age. This indicates a change in allocation patterns in these shrubs with greater allocation to leaf than stem material. Since these shrubs, either unfertilized or fertilized with Plantosan plus urea, had lower shoot/root dry mass ratios (Table 5.3) compared with shrubs fertilized with Plantosan plus ammonium sulphate, it is likely that the change in allocation patterns, with more resources directed to the roots, was at the expense of stem material.

Time series changes in allocation patterns in above-ground biomass and between above- and below-ground biomass have been recorded in a number of species of *Pinus* (Madgwick, Jackson and Knight, 1977; Pearson, Fahey and Knight, 1984). However, changes are slow and can be attributed to a number of environmental factors (Landsberg, 1986). In the current study, both shrub age and nutrient availability were shown to influence these allocation patterns.

Leaf area, leaf area index and leaf longevity

Similar to an increase in mean leaf area of *Leucospermum parile* following nitrogen fertilization (Witkowski *et al.*, 1990a), the total leaf area of *P. neriifolia* shrubs did increase, from 3.5 m^2 in six year old shrubs to 11.8 m^2 in unfertilized ten year old shrubs. The total leaf area of shrubs fertilized with Plantosan plus ammonium sulphate and Plantosan plus urea was 16.8 and 16.1 m^2, respectively. This shows that the total leaf area increased both as a result of increasing shrub age and as a result of applied inorganic fertilizers. This is despite the leaf area (expressed as leaf area per stem cross-sectional area) of shrubs in this investigation not showing variation with age or between fertilizer treatments. This shows that there was more leaf production with age and as a result of applied fertilizers but that this increased leaf production was at the expense of comparable amounts of stem material produced to carry the leaves. There was significant seasonal variation in leaf area (per stem cross-sectional area) although this did not change with age or fertilizer applications (Figures 3.2 and 5.2). The seasonal variation that did occur was probably as a result of new leaf production (leaf area low), new leaf expansion (leaf area high), and finally stem thickening and leaf loss (leaf area low). Although seasonality in leaf area of this kind has not been reported for the Proteaceae, it is not uncommon, particularly in non-evergreen plants (Chabot and Mooney, 1985). Casual observations show that this is also true for local evergreen trees.

In Section 5.1 it was reported that there were no changes in leaf area ratio with age or as a result of the application of inorganic fertilizers. There were, however, age related changes in leaf area index which were greater in fertilized than unfertilized shrubs (Tables 3.2 and 5.4). Common leaf area indices in mediterranean ecosystems are 1-2 increasing to 3-4 with increases in soil water (Cody and Mooney, 1978 loc. cit. Miller, 1983). In this study, total precipitation and precipitation distribution prior to (1984-1987) and after (1987-1989) the application of inorganic fertilizers showed no significant differences (Figures 2.4 and 2.5). Therefore, the increases in leaf area index were probably the result of other environmental factors, possibly nutrients, since the leaf area index of fertilized shrubs was significantly greater than that of unfertilized shrubs (Table 5.4). The positive influence of inorganic fertilizers on leaf area index has been reported in certain forest plants (Landsberg, 1986). In addition, leaf area index in the oak (*Quercus robur*) is known to increase sharply to a maximum in the first 30 years (Jarvis and Leverenz, 1983). The increases in leaf area index in cultivated *P. neriifolia* are, therefore, age related, although the addition of nutrients (fertilization) also influences leaf area index.

Although leaf area indices for cultivated *P. neriifolia* are comparable with leaf area indices (between 1 - 4) for mediterranean ecosystems (including fynbos), for all ages and fertilizer treatments, leaf area index was lower than for other plant life forms, for example, deciduous (6) and coniferous (18 - 20) forests (Grier and Running, 1977). As stated earlier, data calculated for *P. neriifolia* refer to individual shrubs and not whole communities. The comparative data cited above refer to commercial forest communities with higher plant densities than in the protea orchard.

Increased sclerophylly of leaves is a response to low soil nutrient availability and may lead to increases in leaf longevity (Grubb, 1977). Specific leaf area was calculated for certain leaves and showed the largest decrease over a 32 month period in unfertilized shrubs. While the specific leaf area of shrubs fertilized with Plantosan plus urea also showed a slight decline, in shrubs fertilized with Plantosan plus ammonium sulphate, specific leaf area remained constant. Declines in specific leaf area were probably as a result of increased leaf thickness and are indicative of an increase in leaf sclerophylly. Since the decline in specific leaf area was greatest in unfertilized shrubs and since leaf area index in fertilized shrubs was greater than in unfertilized shrubs, this increase in sclerophylly was greater in unfertilized shrubs, probably in response to increasingly lower levels of available nutrients in the soil (Table 5.8). This is consistent with age related increases in leaf/stem dry mass ratios for unfertilized shrubs discussed earlier.

Leaf longevity was not affected by the application of inorganic fertilizers and the mean number of tagged leaves present after 32 months was 42% (Figure 5.3). This relatively long leaf lifespan of cultivated *P. neriifolia* is similar to casual observations of the leaf lifespan of *P. neriifolia* in its natural habitat (Rourke, personal communication) and is consistent with the increase in leaf area index with time described above. However, in the genus *Protea*, some species have leaves that live for only one year, whereas in other species leaves may live for as long as six years (Kruger, 1981).

Leaf longevity is indicative of resource availability and environmental growth conditions (Miller, 1983). Generally, increased leaf longevity is a phenotypic response to nutrient stress in evergreen trees and shrubs (Specht and Groves, 1966; Miller, Cooper and Miller, 1976). In mediterranean ecosystems the length of the summer drought and availability of nitrogen and phosphorus are major determinants of leaf lifespan (Miller, 1983) with drought deciduous leaves having shorter lifespans than their sclerophyllous counterparts (Westman, 1983). The nitrogen and phosphorus applied as inorganic fertilizer in the current study did not significantly affect leaf longevity and it may be that slower growing plants are less plastic in their response to environmental changes (Chapin, 1980).

An increased leaf area index and relatively long leaf lifespan also indicate continued production of new leaves with a slow turnover of those leaves already produced. Despite long-lived leaves probably still having a positive carbon balance, a major disadvantage of long-lived leaves is a reduction in photosynthetic rate (Mooney, 1972). This highlights the importance of continued new leaf production as recorded for *P. neriifolia* in this study.

In cultivated populations of *P. neriifolia* (this study) the relatively long leaf lifespan may have been a function of fungicide applications. Prior to 1985, orchards were sprayed with fungicide only after infection was identified. This was generally too late and massive leaf drop due to fungus infection occurred. From 1986 onwards a preventative spray programme, during which fungicides were applied every six weeks, was implemented. The prevention of fungus infection had the result of markedly reducing leaf drop and hence, could be indirectly responsible for the increased leaf longevity. This would also partly explain the low leaf area index recorded for seven year old *P. neriifolia* (measured at a time concomitant with the implementation of preventative fungicide applications) compared to the significantly higher leaf area index of ten year old *P. neriifolia* (measured after three years of preventative fungicide applications).

Flower size, total shoot growth and branching

The dry mass of mature flowers of cultivated *P. neriifolia* varied seasonally with larger and heavier flowers being produced during the peak flowering period and smaller and lighter flowers at both extremities of the flowering season (Figures 3.4 and 5.5). During the peak flowering season plants make use of available resources and favourable environmental conditions (particularly temperature (Kummerow, 1983)) for the production of large flowers. Although there is little seasonal variation in availability of resources at MSNR, high temperatures do not prevail year round, resulting in smaller flowers either side of the peak flowering period. This seasonal variation in flower head dry mass has been observed in a number of the Proteaceae (Personal communication, A.L. Evans, Mount Sheba Nature Reserve, P.O. Box 71, Schagen, 1207, South Africa, and A. Van Eindhoven, Hilltop Flowers, P.O. Box 1203, Nelspruit, 1200, South Africa). Furthermore, mature flowers from fertilized shrubs were heavier than those from unfertilized shrubs although this was manifested only two years after fertilizer applications were initiated (Figure 5.5). Of interest is that flower head mass of *P. neriifolia* flowers varies widely. The mean flower head dry mass (inclusive of all seasons) for both fertilized and unfertilized cultivated *P. neriifolia* shrubs in this investigation was 42 g, compared to 50 g (Claassens, 1986) and 21 g (Low and Lamont, 1986) for unfertilized wild *P. neriifolia* plants.

Although there exist only limited comparative data for other members of the Proteaceae, it is interesting to note the effects of inorganic fertilization on the shoot growth and flowering of *P. neriifolia* shrubs cultivated in a summer rainfall area. The mean monthly growth of primary and lateral shoots decreased with increasing age of the shrubs although this decrease in shrubs receiving inorganic fertilizers was not statistically significant (Table 5.5). This age series decrease in total shoot growth is common in the Proteaceae (Rourke, personal communication), although inorganic fertilizers do have a positive effect in the production of longer stemmed shoots (Table 5.5). Similarly, increases in shoot extension in response to nitrogen fertilization were found during the first seasons growth of *Leucospermum parile* (Witkowski *et al.*, 1990a). In contrast to increased branching in *Leucospermum parile* with additions of nitrogen and a mixture of all essential nutrients (Witkowski *et al.*, 1990a), the rate of lateral shoot production of cultivated *P. neriifolia* did not appear to change significantly with age or due to the application of inorganic fertilizers. However, there was a significant increase in the number of flowers produced per shrub, both with increasing age of the shrubs and as a result of the application of inorganic fertilizers (Table 5.5). Increased production of flowers in response to inorganic fertilizers is particularly important since the dry mass of flowers from fertilized shrubs was significantly greater than that from unfertilized shrubs.

In summary, therefore, the growth and architectural responses to inorganic fertilization by *P. neriifolia* cultivated in a summer rainfall area were comparable with those of slow growing evergreen shrubs, including certain species of Proteaceae, from nutrient poor mediterranean ecosystems (Specht, 1963; McMaster, Jow and Kummerow, 1982). It would appear that fynbos shrubs are well adapted to low levels of available nutrients and exhibit a low degree of morphological plasticity. However, some change in allocation patterns, both age and nutrient related, were observed in this study.

6.3.2 Phenology

Growth periodicities are adaptations to seasonal stress on plant growth (Bond, 1980). In the phenological model developed by Specht *et al.* (1981) and Specht *et al.* (1983) nutrient availability is considered to be the major determinant of shoot development in mediterranean-type heathlands on strongly leached, nutrient poor soils. Shoot growth in heathland overstorey species occurs in late spring/summer at the expense of nutrients released from litter decomposing in spring. Leaf drop coincides with shoot growth. The overstorey species of mediterranean shrublands growing on moderately leached, relatively fertile soils are not subject to severe nutrient limitation and shoot growth occurs in spring, prior to leaf fall in the summer.

Phenological studies of *P. neriifolia*, a heathland overstorey species, in its natural habitat have shown shoot growth in late spring/early summer (November/December) and peak flowering in autumn/early winter (April/May/June) (Mostert, Siegfried and Louw, 1980; Kruger, 1981; Pierce, 1984). When this species was cultivated in the summer rainfall area of the eastern Transvaal highlands there was a shift in these phenophases (Heinsohn and Pammenter, 1988). Shoot growth peaked in late winter/early spring (August/September/October) and flowering in autumn (March/April/May) (Figure 3.4). Given the earlier shoot growth, the earlier flowering is not surprising: inflorescences are terminal and so flowering will follow shoot growth. Proteoid root growth showed seasonality coincident with that of shoot growth with maximum occurrence of proteoid roots between August and November (late winter/spring) (Figure 3.7). Litter production also showed seasonal trends with peak litter production occurring between July and September (winter/early spring)

(Figures 3.9 and 5.6), slightly earlier than the peak in shoot growth. This period of litter production is in marked contrast to the highly synchronous summer peak in litter production by more than 90% of the Proteaceae studied in the fynbos (Kruger, 1981; Mitchell and Coley, 1987; Witkowski, 1989a). For *P. repens* this summer peak in litter production did not appear to be affected by soil moisture (Mitchell and Coley, 1987). Leaf litter decomposition was not seasonal (Figure 3.11) but slow, with slow release rates of nitrogen, phosphorus and potassium (Figure 3.14). As in the case of *P. repens* (Mitchell and Coley, 1987), *P. neriifolia* leaf litter decomposition rates are slower and not significantly seasonal compared with those of sclerophyllous shrubs of other mediterranean ecosystems (Schlesinger and Hasey, 1981; Specht, 1981). It is unlikely, therefore, that current seasons' vegetative growth would occur solely at the expense of nutrients released from the litter of the previous season, an assumption implicit in the model of Specht *et al.* (1981) and Specht *et al.* (1983).

The shift in phenophase of *P. neriifolia* observed in this study compared to its natural habitat is what would be predicted by Specht's model if the species was grown in a moderately leached soil with no nutrient limitation. However, the MSNR soils are highly leached and as nutrient poor as strongly leached heathland soils (Tables 2.1 and 2.2, and Section 2.1.2). Furthermore, in the absence of fertilizer applications, available soil nutrient levels did decline (Table 5.8). Two *Protea* species, *P. roupelliae* and *P. caffra* occur naturally in the Mount Sheba area. Although shoot growth occurs throughout the year in *P. roupelliae*, both species show a peak during spring (September to November) (personal observation). This is the phenological pattern predicted by Specht's model for species growing on strongly leached, nutrient poor soils. It would appear, therefore, that the shift in phenophase observed in growing *P. neriifolia* in the eastern Transvaal highlands was not a response to higher nutrient availability. This is consistent with the findings that when inorganic fertilizers were applied, phenophases did not shift to those characteristic of more fertile soils (Section 5.2.1). Furthermore, nutrient additions had no effect on the vegetative phenology of *Leucospermum parile* (Witkowski *et al.*, 1990a). However, it is implicitly assumed in Specht's model that growth is at the expense of concurrently absorbed and utilized nutrients and the possibility of the utilization of previously absorbed and stored nutrients (Groves, 1965) is ignored. The age-related changes in shrub nutrient concentrations presented in this thesis strongly suggest growth at the expense of stored nutrients. Therefore, although the model of Specht *et al.* (1981) and Specht *et al.* (1983) may be applicable to evergreen sclerophyllous shrubs growing in mediterranean ecosystems, it cannot explain the observed shift in phenophases when *P. neriifolia* is grown on nutrient poor soils in a summer rainfall area. Lastly, the possibility of the control of phenological events by environmental factors other than nutrient availability cannot be ignored. Further, although endogenous rhythms within the plant may be important in controlling phenophase events (Pierce, 1984), they do not explain the shift in phenophases observed in *P. neriifolia* at MSNR.

Kummerow (1983) has proposed an alternative model to explain the growth of sclerophyllous vegetation in mediterranean ecosystems. This model suggests temperature and soil moisture as phenophase determinants: shoot growth and flowering are temperature dependent (higher temperatures promoting greater shoot growth and flower development) while root growth and litter production are soil moisture dependent (higher soil moisture levels promote fine root growth while lower soil moisture levels result in higher leaf litter loss (Kummerow, 1983). The findings of the present study may be explained partly by temperature and soil moisture.

Shoot growth of *P. neriifolia* cultivated in a summer rainfall area peaked in late winter/early spring (August to October) and flowering in autumn (March/April/May) (Figure 3.4). Maximum proteoid root occurrence was between August and November (late winter/spring) (Figure 3.7) and litter production peaked between July and September (winter/early spring) (Figures 3.9 and 5.6), slightly earlier than the peak in shoot growth. Shoot growth was greatest during the period of increasing temperatures (Figures

2.4 and 2.5) although there was continuous but less intense shoot growth throughout the year (Figure 3.4). Flower development occurred during the season of highest temperature (Figures 2.4 and 2.5) with maximum flower production in autumn, prior to the onset of the coolest temperatures of the year (Figures 2.4 and 2.5). Although proteoid root growth was greatest during the period of lowest rainfall (Figures 2.4 and 2.5), soil water content (Figure 3.8), due to the plastic mulch, did not change much during the year. Peak litter production occurred in winter/early spring when soil moisture was lowest (Figure 3.8) (although as for proteoid root growth, the black plastic mulch results in similar soil moistures throughout the year).

Similar shifts in phenological events were recorded in the growth of overstorey plants in mediterranean ecosystems in the south-eastern Cape of South Africa (Pierce and Cowling 1984a). As with the seasonal growth of these plants, the model proposed by Kummerow (1983) does explain partly the observed shift in phenophase in *P. neriifolia* cultivated in a summer rainfall area. However, the influence of the plastic mulch on soil water, the timing of proteoid root growth and litter production require elucidation. Further, the model proposed by Specht *et al.* (1981) and Specht *et al.* (1983) cannot be ignored since the seasonal regime of the habitat (for example, the availability of nutrients through litter production and the effects of the climate on decomposition (Bond, 1980)) will, to some degree, determine plant growth and growth periodicity. Although nutrient availability in the soils at MSNR did exhibit seasonal variation, this variation was not consistent with the model of Specht *et al.* (1981) and Specht *et al.* (1983). That shifts in phenophase observed in *P. neriifolia* cultivated at MSNR were not a response to nutrient availability was shown by the lack of influence of inorganic fertilizers on the timing of phenological events.

Possible advantages of the late winter/early spring shoot growth in *P. neriifolia* cultivated in a summer rainfall area can be suggested. It is not known at what stage of development leaves of *P. neriifolia* start to transpire and photosynthesize. If early shoot growth does not have a high water cost, early shoot growth in a summer rainfall area results in a full complement of photosynthesizing tissue when air temperatures and soil water conditions become suitable for rapid photosynthesis. Additionally, early shoot growth will result in the completion of a disease-vulnerable growth phase before the onset of the wet period with the associated increase in the incidence of pathogens.

Litter decomposition rates and rates of nutrient release from decomposing litter have been reported to be slow (Figures 3.11, 3.12, 3.13 and 3.14). Although comparable to decomposition rates of *P. repens* litter (Mitchell and Coley, 1987), these rates are slower than those of other mediterranean ecosystems (Schlesinger and Hasey, 1981; Specht, 1981). In this investigation, litter bags with a mesh size of 2 mm were used. It has been reported that in litter decomposition studies, the use of litter bags with a small mesh size, such as 2 mm, may exclude macrofauna that may accelerate the decomposition process (Steenkamp, 1991). Although the influence of mesh size was not investigated, it should be noted that faster protea leaf litter decomposition rates may be attained using litter bags with a larger mesh size. Also, although not quantified in the current investigation, the use of plastic mulch and pesticides in the cultivation process may have contributed to the slow leaf litter decomposition rates recorded.

6.4 Plant and soil nutrient status

6.4.1 Plant

Nitrogen

The seasonal variation in leaf and stem nitrogen concentrations of cultivated *P. neriifolia* was more evident in younger than in older shrubs and the application of inorganic fertilizers did not appear to alter this phenomenon (Section 5.4.1). When seasonal variation was recorded (Figure 3.15a), greatest leaf and stem nitrogen levels were recorded in late winter/spring immediately prior to the peak in maximum vegetative growth (Figure 3.4). Similar peak nitrogen levels were found in the florets and bracts of *P. neriifolia* prior to and after the application of inorganic fertilizers (Figures 3.15b and 5.9), although peak nitrogen levels were slightly later than in the leaves and stems. Again, since flowers are terminal, this is to be expected. Observations of seasonal variations in the nitrogen levels of *P. neriifolia* tissue is in accordance with seasonal variations in leaf nitrogen concentrations in Californian chaparral (Shaver, 1983).

The concentration of nitrogen in the various shrub tissues of P. *neriifolia* varied among tissue types, with age, and with the application of inorganic fertilizers (Figures 3.15, 5.8 and 5.9). The greater leaf, stem and flower nitrogen concentration in shrubs fertilized with ammonium sulphate compared with the other treatments suggests the absorption of nitrogen in excess of that required for immediate growth (Figures 3.15, 5.8 and 5.9). This is not uncommon in the Proteaceae with *Leucospermum parile* using both the leaf and twig organs for the storage of this excess nitrogen (Witkowski *et al.*, 1990a). While stem and flower nitrogen levels in shrubs unfertilized and shrubs fertilized with Plantosan plus urea were comparable to levels in the corresponding tissue types in shrubs prior to the application of inorganic fertilizers, leaf nitrogen levels were approximately 50% lower. This suggests that the shrubs fertilized with Plantosan plus urea did not readily incorporate the nitrogen in the urea and that growth was at the expense of stored nitrogen. In contrast, the increase in the nitrogen concentration of floral tissue of shrubs fertilized with Plantosan plus urea indicates some nitrogen incorporation by these shrubs. However, since urea contains more nitrogen than ammonium sulphate, it is possible that this nitrogen is not as readily available to the Proteaceae as nitrogen in the ammonium form.

In both unfertilized and fertilized shrubs, the mean nitrogen, phosphorus and potassium concentration in each tissue type was significantly greater than the nutrient level in the corresponding tissue type of a range of unfertilized *Protea* species growing in their natural habitat (Low and Lamont, 1986). Similarly, shoot nitrogen concentrations of both unfertilized and fertilized *P. neriifolia* shrubs was greater than shoot nitrogen concentrations in *Leucospermum parile* growing in its natural habitat with and without nutrient additions (Witkowski *et al.*, 1990a).

Phosphorus

Trends similar to nitrogen were found in phosphorus concentrations between tissue types, shrub age and fertilizer treatments (Figures 3.16, 5.10 and 5.11), with phosphorus levels of vegetative plant parts greatest immediately prior to the peak in vegetative growth (Figure 3.4). As with floral nitrogen concentrations, peak floral phosphorus concentrations followed closely peak vegetative phosphorus concentrations (Figures 3.16, 5.10 and 5.11). This seasonal variation in tissue phosphorus levels is similar to that recorded in Californian chaparral viz. an increase in winter and spring (Shaver, 1983), the period of active vegetative growth, followed by a sharp decrease in summer (Shaver, 1983), a period of reduced vegetative growth.

The phosphorus concentration was greatest in leaves, followed by similar concentrations in stems and flowers. However, of interest is that the phosphorus concentration of all tissue types was greater than that recorded for a range of unfertilized *Protea* species growing in their natural habitat (Low and Lamont, 1986) but comparable to shoot phosphorus levels recorded for unfertilized and fertilized *Leucospermum parile* growing in its natural habitat (Witkowski *et al.*, 1990a).

Potassium

In general, *P. neriifolia* potassium levels did not show significant seasonal variations between tissue types, shrub age and fertilizer treatments (Figures 3.17, 5.12 and 5.13), with significant seasonal variation in certain floral parts only. In these cases the highest floret and bract potassium concentration was recorded in July and November (winter/spring) and lowest levels occurred between February and March (late summer/autumn). It would appear, therefore, that potassium levels are greatest immediately prior to the onset of flower bud set, and that these levels decline with the development of the flower. The lack of seasonal variation in potassium levels in vegetative plant tissue suggests that Proteaceae have sufficient potassium for growth and that the nutrient is not growth critical (Claassens and Foelscher, 1980).

Statistical analysis showed that despite some variation, particularly in floral tissue, the levels of potassium in the various tissue types were of the same order prior to and after the application of inorganic fertilizers (Figures 3.17, 5.12 and 5.13). It is likely, therefore, that the shrubs absorb only as much potassium as is required for immediate growth (vegetative and reproductive). This is in accordance with the statement by Claassens and Foelscher (1980) that potassium is not a critical nutrient in the growth of Proteaceae. In support of this is the finding that the potassium levels of the various tissue types recorded in this investigation were of the same order as those recorded for a range of unfertilized *Protea* species growing in their natural habitat (Low and Lamont, 1986).

Seasonal variations in proteoid and non-proteoid root nitrogen, phosphorus and potassium concentrations could not be studied due to the premature death of the study shrubs (Section 2.1.4).

Summary

The seasonal variations in plant tissue nitrogen, phosphorus and potassium levels in *P. neriifolia* cultivated in a summer rainfall area support the hypothesis that nutrient uptake during winter is a major nutrient pathway in mediterranean-type vegetations (Shaver, 1983). Nitrogen and phosphorus (and to a lesser extent, potassium) levels were highest in all tissue types during the winter/spring period. Proteoid root occurrence and above-ground vegetative growth are also highest during this late winter/spring period. Further, peak litter production was recorded during the winter/spring period. However, it was shown that above-ground vegetative growth in winter/spring was unlikely to be at the expense of concurrently absorbed nutrients by proteoid roots in their greatest abundance. Rather, it is likely that growth was at the expense of previously absorbed nutrients. This results in maximum nutrient concentrations in above-ground vegetative tissue types. While the nutrient content of these tissue types remains relatively constant, nutrient concentration decreases with elongation and maturation of the tissues. Flower nutrient concentrations are greatest at the time of flower bud set. Similarly to leaves and stems, while the nutrient content remains relatively constant, nutrient concentration decreases with flower development. Due to the slow decomposition of the leaf litter of *P. neriifolia*, it is unlikely that, as speculated by Specht *et al.* (1981) and Specht *et al.* (1983), nutrients absorbed in winter/spring by the proteoid roots are nutrients released from the previous seasons leaf litter (which shows a peak in winter/spring, immediately prior to and concomitant with maximum nutrient absorption). It is interesting to note that maximum nutrient absorption did not appear to occur at a time when soil nutrients were available in their highest levels (viz. spring/late summer).

Comparisons with mediterranean ecosystems show considerable year to year variation (Mooney and Rundel, 1979; Shaver, 1983) and highlights the necessity of measuring seasonal trends for at least two years (as in this study). This is important as plant growth may be site specific and abiotic factors such as temperature and light will also influence plant behaviour.

Changes in leaf nutrient levels with age

Changes in the nitrogen and phosphorus levels with age of leaves of cultivated *P. neriifolia* were similar to those reported for a number of plants of mediterranean ecosystems (Specht and Groves, 1966; Gulmon, 1983). There is limited comparative data for changes in leaf potassium levels but the initial drop in leaf potassium levels was expected as part of the general redistribution pattern of nutrients from older to younger leaves. However, the accumulation of potassium in older leaves (Figure 5.4c) was unexpected. During rain, potassium levels in shrub throughfall and stemflow are higher than in rainwater (Table 5.9). While part of this potassium would be from dry matter fallout, due to potassium re-accumulation in the leaves, there could be leaching of potassium from the leaves. Although not quantified in the current investigation, this is in accordance with the finding that potassium is removed from leaves largely by leaching and not by retranslocation (Morton, 1977; Chapin, Johnson and McKendrick, 1980 loc. cit. Chapin, 1980).

The redistribution of nitrogen and phosphorus from older to younger leaves is a common resource economising strategy in a number of heathland (Specht and Groves, 1966) and non-heathland (Miller *et al.*, 1976) plants. Interestingly, the application of inorganic fertilizers did not significantly affect the redistribution of nitrogen, phosphorus or potassium. (Figure 5.4).

6.4.2 **Soil**

The soils of MSNR (Table 2.1) are well drained and highly leached, and a comparison with nutrient data presented by Specht and Moll (1983) and Pierce and Cowling (1984a,b), and criteria proposed by Day (1983) (Table 2.2) show the soils of MSNR to be as nutrient poor as strongly leached heathland soils. The possible exception is total nitrogen which, at 0.14% is marginally higher than the 0.12% proposed by Day (1983) as the upper limit of nutrient poor heathland soils. As in the case of fertilizer additions to coastal sand-plain fynbos (Witkowski, Mitchell and Stock, 1990b), the application of inorganic fertilizers did improve the soluble and total nitrogen and available phosphorus status of the soils although not to the extent described by Witkowski *et al.* (1990b). Cation concentrations remained constant (Table 5.8) and unfertilized soils showed signs of depletion, particularly a depletion in soluble nitrogen levels (Table 5.8). The relative stability of soil pH was similar to that described by Witkowski *et al.* (1990b).

In both cases the depth to which the soil was sampled was 200 mm and, although not studied in this investigation, excess nitrogen from the inorganic fertilizers not utilised by the *P. neriifolia* shrubs was probably lost from the 0 - 200 mm layer through leaching (Witkowski *et al.*, 1990b). However, it is important to note that the Table Mountain sandstones of MSNR have a higher clay content than the sand-plain soils, and that this would reduce the leaching rate through the MSNR soil profile. Since phosphorus is a relatively immobile element (Bieleski, 1976 loc. cit. Witkowski *et. al.*, 1990b), it is likely that excess phosphorus was bound in the soil and, therefore, unavailable to the plants. The relative stability of the concentrations of the major cations, for example, potassium, was probably as a result of nutrient leaching down the soil profile, as in the case for nitrogen.

Significant seasonal trends in soluble and total nitrogen, available phosphorus and available potassium were recorded in the MSNR soils and since this was similar prior to and after the application of inorganic fertilizers (Figures 3.18 and 5.14), the application of inorganic fertilizers did not affect the seasonal availability of these three nutrients. Since most heathland communities are developed on soils of low nutrient status and low pH, a large fraction of the nitrogen and phosphorus in these soils is contained in the organic component (as indicated by total nitrogen and phosphorus recorded at MSNR). Nitrogen and phosphorus are slowly released from the organic component by microbial action resulting in seasonal flushes of these nutrients (Woolhouse and Kwolek, 1981). It is likely that this microbial action would be temperature related (Woolhouse and Kwolek, 1981) and, furthermore, soil moisture would also be important in determining the seasonal availability of the nutrients. Interestingly, therefore, seasonal 'abundance' of soluble nitrogen and available phosphorus in a summer rainfall area occurred in the wetter and warmer months of the year (Section 5.4.2). As has been stated earlier, seasonal variations in the availability of nutrients from the soil were not consistent with the phenological models of Specht *et al.* (1981) and Specht *et al.* (1983). Also, maximum nutrient absorption by shrubs did not appear to occur at times when soil nutrient concentrations were highest.

6.5 Nutrient budgets

Internal and external nutrient cycling in nutrient poor mediterranean ecosystems has been described as efficient, particularly for the two most studied nutrients, nitrogen and phosphorus (Gray and Schlesinger, 1981; Groves, 1983; Mitchell, 1983). Studies on the fynbos shrub *P. neriifolia* cultivated in a summer rainfall area suggest that, although fire is excluded, this shrub does exhibit efficient nutrient cycling strategies under cultivation. Further, under cultivation, flowers are removed for commercial sale. This results in large nutrient loss from the system, and it appears that nutrient input to the system is inadequate to replace this loss. Inorganic fertilizer applications do go some way to redress this loss.

Nitrogen, phosphorus and potassium were selected for study in this investigation because they are the three macronutrients that most likely affect the growth of the Proteaceae (Claassens, 1981; Claassens and Foelscher, 1980; Claassens, 1986), and nitrogen and phosphorus are regarded as the two nutrients most growth limiting in mediterranean ecosystems (Groves, 1983). In this investigation the cycling of the three selected nutrients has been presented in a simplified form: inputs from rainfall and inorganic fertilization, throughputs of rainfall via canopy throughfall and stemflow, fluxes via litter production and decomposition, the uptake of nutrients by above- and below-ground biomass, and losses through stream-water and the harvesting of flowers for commercial sale (Figures 3.19, 5.15, 5.16 and 5.17).

It is important to note that in the current investigation nutrient budgets are presented on an hectare basis, assuming a planting density of 1 000 shrubs per hectare. However, budgets refer to the protea component only and do not include the considerable grass and forb communities in the inter-row. Furthermore, rainfall, shrub throughfall, stemflow and stream-water nutrient data are limited because of storage and analysis difficulties described earlier (Section 2.4.3).

6.5.1 **Inputs**

Rainfall

Other than nutrient inputs through inorganic fertilization, the only input into the cultivated *P. neriifolia* system studied in this investigation was that through rainfall, inclusive of dry matter fallout (Tables 3.6 and 5.9). One of the main sources of nitrogen entering the plant/soil system is via precipitation (Groves, 1983) and although measurements in this study were limited, the input of nitrogen via rainfall (Figures 3.19a, 5.15a, 5.16a and 5.17a) was approximately 4 times greater than the total nitrogen input via precipitation at the coastal sandy plain fynbos study site at Pella in South Africa (Stock and Lewis, 1986a). Since the mean annual rainfall at the MSNR study site (Figures 2.4 and 2.5) is approximately twice that of the Pella site (Stock and Lewis, 1986a), the nitrogen input 4 times greater suggests a higher nitrogen concentration in the rainfall in the summer rainfall area (MSNR). The annual input of total nitrogen via rainfall at the MSNR study site was also greater than the 71 - 142 mol ha^{-1} yr^{-1} estimated for mediterranean regions (Rundel *et al.*, 1983) but similar to total nitrogen inputs in higher rainfall European heathlands (Robertson and Davies, 1965). Although nitrogen fixation was not studied in the current investigation, as with other mediterranean ecosystems (Rundel *et al.*, 1983), nitrogen fixation rates are thought to be low at MSNR. Mean phosphorus inputs via rain at MSNR was 12 mol ha^{-1} yr^{-1} (Figures 3.19b, 5.15b, 5.16b and 5.17b) which is less than half that estimated for British heathlands (Groves, 1983). Comparative data do not exist for other mediterranean ecosystems but for nutrient poor South African and Australian soils, a mean annual rainfall of 400 mm is estimated to deliver only 0,0035 ppm phosphorus per metre depth of soil per 1 000 years (Rundel *et al.*, 1983). Other sources of phosphorus, for example, the weathering of parent rock, are thought to be more important than phosphorus acquisition via precipitation (Rundel *et al.*, 1983). This was not studied in this investigation. Potassium input via rainfall (approximately 186 mol ha^{-1} yr^{-1}) (Figures 3.19c, 5.15c, 5.16c and 5.17c) was relatively high compared to both nitrogen and phosphorus inputs by the same route. There are no comparative data for mediterranean ecosystems but potassium rainfall levels are approximately double those recorded on Marion Island (Smith, 1985). This higher level of potassium at MSNR is not surprising considering the relative isolation of Marion Island and the overwhelming marine influence on the chemical composition of the precipitation (Smith, 1985).

Inorganic fertilizers

Shrubs fertilized with Plantosan plus ammonium sulphate and Plantosan plus urea received additional nutrients from these fertilizers. Compared with the input of nitrogen, phosphorus and potassium from rainfall, input of these nutrients through inorganic fertilizer applications was high (Figures 5.15 and 5.16). Inputs of nitrogen in plants fertilized with Plantosan plus ammonium sulphate (33 425 mol ha^{-1} yr^{-1}) and Plantosan plus urea (59 685 mol ha^{-1} yr^{-1}) were 9 times and 17 times greater, respectively, than fertilizer inputs studied on *Leucospermum parile* (Witkowski *et al.*, 1990a). Similarly, phosphorus inputs via both fertilizer types (2 125 mol ha^{-1} yr^{-1}) were 12 times greater than phosphorus fertilizer inputs studied in *L. parile*

(Witkowski *et al.*, 1990a). Inputs of nitrogen from applied fertilizers were also considerably higher than those of Specht (1963), although phosphorus levels were comparable to latter fertilizer applications of Specht (1963) in studies on the effects of fertilizers on Australian heathlands. Phosphorus levels supplied in this investigation were, however, higher than the 700 mol ha^{-1} yr^{-1} upper limit for long-lived overstorey species (for example, *Banksia ornata*) suggested by Heddle and Specht (1975). Potassium inputs through fertilizer applications were the same for both fertilizer types (4 800 mol ha^{-1} yr^{-1}) and were in balance with the nitrogen and phosphorus levels (Section 4.3). Comparative data for potassium fertilization in mediterranean ecosystems are not available but since proteas are tolerant of relatively high salinities (Claassens and Foelscher, 1980; Claassens, 1986), possible toxicity responses to potassium fertilization were not envisaged.

6.5.2 Nutrient pool sizes

Plant

Nitrogen, phosphorus and potassium nutrient pools in the above-ground biomass are greater than those in the below-ground biomass for *P. neriifolia* shrubs of all ages, for all fertilizer treatments (Figures 3.19, 5.15, 5.16 and 5.17). However, the ratio of above-ground to below-ground pools does decrease in ten year old shrubs growing on soils with lower nutrient concentrations (for example, shrubs fertilized with Plantosan plus urea and unfertilized shrubs (Figures 5.16 and 5.17)). This is in contrast to nitrogen and phosphorus distribution between above- and below-ground biomass in 15 year old heath in south-eastern Australia, where nutrient pools in the below-ground biomass were 3.5 times greater than those in the above-ground biomass (Specht, Rayson and Jackman, 1958). There exist no comparative data for the fynbos or the Proteaceae. However, nitrogen, phosphorus and potassium pools in the above-ground biomass of Proteaceae growing in their natural habitat are similar to those recorded in this investigation (Low, 1983; Low and Lamont, 1986), although the age of shrubs does influence comparisons. This is particularly apparent in inputs into the litter nutrient pool of *P. repens* and *P. neriifolia* growing in their natural habitat. Nitrogen, phosphorus and potassium inputs in 17 and 21 year old shrubs are up to ten times larger than the corresponding inputs in ten year old *P. neriifolia* shrubs in this investigation (Figures 5.15, 5.16 and 5.17 c.f. Low, 1983; Low and Lamont, 1986). The age effect is more clearly seen when data from this investigation are compared with fynbos data of Van Wilgen and le Maitre (1981). Pool sizes of above-ground biomass increase sharply with shrub age and also vary considerably between locations. However, as in the current study prior to the application of inorganic fertilizers (Figure 3.19), pool sizes in the above-ground biomass reflect the low levels of essential nutrients typical of the fynbos sites (Van Wilgen and le Maitre, 1981).

The total nitrogen, phosphorus and potassium in the biomass of shrubs increased with increasing age of the shrubs and due to the application of inorganic fertilizers, particularly the ammonium sulphate supplemented fertilizer preparation (Figure 5.15). It is likely, therefore, that cultivated *P. neriifolia* responded primarily to nitrogen fertilization and that ammonium nitrogen was more readily available to the shrubs than nitrogen in the urea form (Figure 5.16). Similarly, fertilized *Leucospermum parile* responded primarily to additional nitrogen although in that case nitrogen was supplied as a mix of ammonium and nitrate nitrogen (Witkowski *et al.*, 1990a).

Soil

In fertilized shrubs, soil soluble and total nitrogen pools increased as a result of the application of inorganic fertilizers. Since Plantosan plus urea contained the most nitrogen, it was not surprising that soil soluble and total nitrogen pools of these shrubs were highest (Figure 5.16a). Although nitrogen (soluble and total) pools in soils of shrubs fertilized with Plantosan plus ammonium sulphate (Figure 5.15a) were lower than those of shrubs fertilized with Plantosan plus urea (Figure 5.16a), they were greater than soil nitrogen (soluble and total) pools of shrubs prior to fertilizer applications (Figure 3.19a) and unfertilized shrubs (Figure 5.17a). The possible depletion of soil nitrogen was illustrated by lower soil (soluble and total) nitrogen pools in unfertilized shrubs (Figure 5.17a) compared with shrubs prior to the application of inorganic fertilizers (Figure 3.19a). Soil available phosphorus pools also increased as a result of inorganic fertilization (Figures 5.15b and 5.16b) while soil potassium (available and total) pools did not show any response to applied fertilizers (Figures 5.15c and 5.16c). The influence of fertilization on soil nitrogen and phosphorus pool sizes was similar to that recorded for fertilization in natural fynbos stands (Witkowski *et al.*, 1990b) although, in the case of the MSNR study site, soils had a higher clay content, possibly resulting in slower leaching of nutrients through the soil profile.

The proportion of nutrients in the total biomass relative to that in the soil total pool is similar to temperate systems and also, more importantly, similar to fynbos.

6.5.3 Losses

Nutrient losses from mediterranean ecosystems can occur by a number of means, for example, soil leaching, runoff, volatilization and particulate loss (Rundel *et al.*, 1983). Soil leaching and particulate loss were not studied in this investigation but are thought to result in only small losses of nutrients from mediterranean ecosystems (Rundel *et al.*, 1983). Although not quantified, in the higher rainfall area of MSNR, soil leaching losses may have been higher (although slower) than for mediterranean ecosystems (Stock and Lewis, 1986a). Volatilization was also not studied in the cultivated *P. neriifolia* system since fire is deliberately excluded from such a system. However, in mediterranean ecosystems, particularly chaparral, fire does result in nutrient loss, particularly of nitrogenous compounds (Chapman, 1967; DeBano and Conrad, 1978; DeBano, Eberlein and Dunn, 1979). Low losses of phosphorus (Debano and Conrad, 1978) and potentially high losses of potassium (DeBano and Conrad, 1978) due to fire have also been reported. In contrast, in preliminary studies at three fynbos sites in South Africa, limited nutrient stock loss through fire was recorded (Van Wilgen and le Maitre, 1981). This is supported by studies at the coastal sandy plain fynbos study site at Pella (South Africa), where the major proportion of the nutrient pools in the above-ground biomass (approximately 3 570 mol ha^{-1} nitrogen and 167 mol ha^{-1} phosphorus) were returned to the soil and surface ash following fire (Brown and Mitchell, 1986; Stock and Lewis, 1986b). While soil runoff after fire may result in nutrient loss, estimates by Van Wilgen and le Maitre (1981) suggest these losses to be small. However, leaching may be exacerbated in fynbos soils which are generally of low clay content (Lamprechts, 1979). Actual losses in smoke and wind-borne ash have not been recorded but may result in significant losses, particularly of nitrogenous compounds (Rundel *et al.*, 1983).

Runoff and soil leaching

In this investigation, losses of nutrients through soil water runoff and leaching were estimated using streamflow estimates and stream-water concentrations. For nitrogen and potassium, these losses were found to be a relatively small fraction (28 and 32%, respectively) of the corresponding nutrient input via rainfall (Figures 3.19a and c, 5.15a and c, 5.16a and c, and 5.17a and c). In contrast, losses of phosphorus (Figures 3.19b, 5.15b, 5.16b and 5.17b) were a relatively large fraction (approximately 79%) of phosphorus input via rainfall. Due to limited rainfall and stream-water data, no comparisons between fertilized and unfertilized systems could be made. In the absence of fire in the cultivated system, soil water runoff would be expected to be relatively low (Rundel *et al.*, 1983). The relatively high loss of phosphorus is probably due to parent rock weathering during rain.

Flower harvest

The major loss of nutrients in the cultivated system occurs through the removal of flowers for commercial sale. With increased age of shrubs there is a corresponding increase in the number of flowers produced with further enhancement as a result of inorganic fertilization. (Figures 3.19, 5.15, 5.16 and 5.17). Measures of nitrogen, phosphorus and potassium loss through flower harvesting in this investigation were considerably larger than estimated nutrient losses by wildflower picking or flower harvest from cultivated *Protea* stands in the Kleinmond and Hermanus area of South Africa (Low and Lamont, 1986). They were also larger than estimates of nutrient removal from unfertilized *P. neriifolia* plants growing in their natural habitat (Claassens, 1986). These differences may be due to shrub age or harvest intensity but this could not be determined as neither was reported by either Low and Lamont (1986) or Claassens (1986).

In the current investigation, losses of nitrogen (Figures 3.19a, 5.15a, 5.16a and 5.17a), phosphorus (Figures 3.19b, 5.15b, 5.16b and 5.17b) and potassium (Figures 3.19c, 5.15c, 5.16c and 5.17c) through flower harvesting represent between 19 and 32% (N), 21 and 33% (P), and 22 and 33% (K) of the respective nutrient pools in the above-ground biomass. The highest proportional loss was in seven year old shrubs prior to the application of inorganic fertilizers (Figures 3.19a, b and c). In ten year old shrubs, both fertilized and unfertilized, proportional losses for each of the nutrients were similar (Figures 5.15, 5.16 and 5.17). The lower proportional loss in these shrubs compared with seven year old shrubs is due to different reasons. For shrubs fertilized with Plantosan plus ammonium sulphate, the above-ground biomass and associated nutrient pools increased, although at proportional rate higher than increased flower production. Therefore, nutrient loss as a proportion of the nutrient pool in the above-ground biomass was lower in the older shrubs. For shrubs either fertilized with Plantosan plus urea or unfertilized shrubs, above-ground biomass did increase with age but was associated with nutrient concentrations in above-ground plant material lower than in seven year old shrubs. This resulted in smaller increases in the nutrient pools in the above-ground biomass of these ten year old shrubs. Similarly, although the number of flowers produced did increase with increasing shrub age, this was also associated with lower nutrient concentrations, resulting in lower nutrient losses from these shrubs. Therefore, nutrient loss as a proportion of the nutrient pool in the above-ground biomass was lower in these shrubs compared with unfertilized seven year old shrubs.

Nutrient losses through flower harvesting were considerably higher than those recorded for *Protea* species and *Banksia hookerana* in their natural habitat (Low and Lamont, 1986). Although there is no comparative age-related data on unharvested shrubs, it is unlikely that these high losses of nutrients from above-ground nutrient pools of cultivated *P. neriifolia* can be sustained given the nutrient poor soils on which the shrubs are grown. This was shown by the reduction in nutrient concentrations of leaves of unfertilized shrubs with increasing age of the shrubs. The application of inorganic fertilizers did alleviate the problem although in this investigation it is likely that the high rate of fertilization (and low rate of recovery in the soil (Table 5.8)) resulted in excess nutrients being leached from the system. This was not recorded.

6.5.4 Nutrient flows

The flow of nutrients within the plant/soil system is important in the maintenance of nutrient cycles (Rundel *et al.*, 1983). In this investigation, three flow paths were studied: rainfall flows, litter production and decomposition, and nutrient assimilation into the nutrient pools in the above- and below-ground biomass.

Rainfall flows

Since older shrubs were larger and intercepted more rainfall, rainfall flows were influenced by shrub age. There were significantly high levels of phosphorus (Figures 3.19b, 5.15b, 5.16b and 5.17b) and potassium (Figures 3.19c, 5.15c, 5.16c and 5.17c) measured in shrub throughfall and stemflow. Although throughfall and stemflow reach the soil and are, therefore, available to the shrubs, relatively high levels of phosphorus were lost from the system through stream-water (Figures 3.19b, 5.15b, 5.16b and 5.17b). This is in contrast to potassium where the potassium in throughfall and stemflow was returned to the soil with low levels in stream-water. Therefore, potassium from throughfall and stemflow is available to the shrubs (Figures 3.19c, 5.15c, 5.16c and 5.17c). Similarly, nitrogen in throughfall and stemflow was returned to the soil where it was available for use by the shrubs (Figures 3.19a, 5.15a, 5.16a and 5.17a).

The importance of shrub throughfall and stemflow possibly lies more in the interception of mist than direct rainfall. As described earlier (Section 2.1.2), MSNR experiences frequent mist, and stemflow, as a result of mist, has been observed to result in large wet areas at the base of the main stem of shrubs (personal observation). Since the plastic mulch is open where the main stem enters the soil, this undoubtedly has a positive influence on the water relations of the shrubs, but could also be important in nutrient input into the soil from shrub throughfall and stemflow. This is particularly important for phosphorus (Figures 3.19b, 5.15b, 5.16b and 5.17b) and potassium (Figures 3.19c, 5.15c, 5.16c and 5.17c) which occur in relatively high levels in shrub throughfall and stemflow. Furthermore, since leaf potassium levels decrease with age (Figure 5.4c), it is possible that potassium is leached from the leaves and, therefore, forms part of throughfall and stemflow.

Litter production and decomposition

In the absence of fire, litter production and decomposition is possibly the most important flow path for nutrient return from the plant to the soil (Schlesinger and Hasey, 1981). In the cultivated system, litter production and decomposition were shown to be important nutrient return mechanisms.

Unlike in studies in fynbos communities in the south-western Cape (Witkowski *et al.*, 1989a), nutrient additions did not result in increased litter production. This was probably as a result of the long lifespan of the *P. neriifolia* leaves, and it is possible that increases in litter production would be detected in future years. As a proportion of the nutrient pools in the above-ground biomass, nutrient loss through litter production in seven year old shrubs was 14, 6 and 2% for nitrogen, phosphorus and potassium, respectively. There was a reduction in this proportion in both fertilized and unfertilized shrubs with increasing shrub age. The greatest reduction (to 3, 1 and 1% for nitrogen, phosphorus and potassium, respectively) occurred in those shrubs receiving Plantosan plus ammonium sulphate. Reductions in shrubs fertilized with Plantosan plus urea and unfertilized shrubs were 6, 1 and 1% and 8, 2 and 1%, respectively, for the three nutrients studied. These proportions indicate the proportion of the above-ground nutrient pools that are circulated through the litter cycle. It is apparent that under relatively 'fertile' conditions of Plantosan plus ammonium sulphate fertilization, proportionately less nutrient is cycled through the litter pathway. This highlights the importance of the litter cycle in shrubs growing on nutrient poor soils.

Since annual decomposition is relatively slow (Figure 3.12), there is an annual build up of litter. For all shrubs, 63, 80 and 82% of the nitrogen, phosphorus and potassium of the current seasons litter accumulate to the respective litter nutrient pools. Although differences related to shrub age and nutrient additions were not studied, litter accumulation provides increasing nutrient pools from which nutrients can be released continuously to the soil. Furthermore, during fire, all nutrients in the litter pool are released (Debano and Conrad, 1978) and the bulk is returned to the soil although losses, as described earlier, may occur. In the absence of flower harvesting, litter production and decomposition, in conjunction with shrub throughfall and stemflow, would be sufficient to provide the necessary nutrients for annual growth (Figures 3.20, 5.18, 5.19 and 5.20). However, flower harvesting upsets the balance in the nutrient cycle and this necessitates the introduction of nutrients from sources external to the plant/soil system, for example, inorganic fertilizers.

Nutrient uptake

Nutrient uptake into nutrient pools in the above- and below-ground biomass was not measured directly, but was calculated from dry mass increases of each component with corresponding nutrient data. Since nutrient uptake is thought to occur during the period of active root growth, this would correspond to the period of greatest proteoid root occurrence viz. late winter/spring (Section 3.2.2). This is similar to that in other fynbos species (Jongens-Roberts and Mitchell, 1986; Stock, Sommerville and Lewis, 1987) although the winter/spring period in the south-western Cape would correspond to higher soil moistures following winter rainfall. Of interest in this study is the increase in nutrient pools in the above- and below-ground biomass with increase in shrub age, and as a result of fertilizer additions. This was greater for shrubs fertilized with Plantosan plus ammonium sulphate (Figure 5.15) than for shrubs fertilized with Plantosan plus urea (Figure 5.16). This suggests a better utilization of nitrogen in the ammonium form than in the urea form. Furthermore, since shrubs fertilized with both fertilizer types received the same levels of phosphorus and potassium, shrubs seem to show a marked response to added nitrogen. This is similar to the growth response of *P. neriifolia* seedlings (Chapter 4) and, in turn, suggests nitrogen is growth limiting in the MSNR soils. As soil total nitrogen is much higher than soil soluble nitrogen, it is probable that it is the transformation of nitrogen to the soluble pool (mineralisation) rather than nitrogen *per se* that is growth limiting. It is also interesting to note the increase in nutrient pools in the below-ground biomass relative to nutrient pool increases in the above-ground biomass in those shrubs growing on soils of reduced nutrient status (Figure 5.17). This is likely to be as a result of increased proteoid root growth in response to low soil nitrogen and phosphorus levels (Kummerow *et al.*, 1978; Lamont, 1972; 1973; 1977; Mooney *et al.*, 1983).

This highlights the importance of proteoid roots in the Proteaceae in maximising absorption of water and nutrients from soils deficient in them (Lamont, 1981). As with proteoid roots in the Proteaceae, specialised root systems are an important component of all shrubs growing in mediterranean ecosystems throughout the world (Lamont, 1981), particularly their role in maximising water and nutrient absorption (Lamont, 1981; Lamont, 1986).

6.6 General conclusions

In the current investigation, growth and nutrient cycling in cultivated *Protea neriifolia* were studied. The shrubs were cultivated in a summer rainfall area and results were compared with data for proteaceous and non-proteaceous plants growing in mediterranean environments. These plants predominate in mediterranean ecosystems, of which species of Proteaceae are major components in fynbos (South Africa) and kwongan (Australian) heath. The primary environmental difference between the MSNR cultivation site and mediterranean ecosystems is the summer rainfall at MSNR.

Cultivation practices also influenced the growth of the cultivated shrubs and as a result, comparisons with natural systems are not always possible. This is because the cultivated system was not homogenous, with the protea component forming only a part of the entire system. The relative contribution of the protea component in any cultivated system depends upon the original planting density of the shrubs. Furthermore, in this investigation, *P. neriifolia* shrubs were cultivated with the aid of plastic mulch. This affected both soil water content beneath the mulch and also influenced plant competition patterns. Other cultivation practices that would also have influenced the growth of *P. neriifolia* are the removal of all flowers during harvest and the spraying of shrubs to reduce pest and pathogen incidence. The relative importance of each has been discussed throughout this thesis.

A further limitation is the experimental design used during the investigation of inorganic fertilization of mature *P. neriifolia* shrubs. However, no alternative was possible as the layout and design of the commercial protea orchard made it impossible to randomly replicate fertilizer treatments. As mentioned earlier, this short-coming in experimental design was overcome by intensively studying the shrubs prior to fertilization.

Despite climatic variations and influences of cultivation practices, a number of general conclusions concerning growth and nutrient cycling of *P. neriifolia* can be made.

The study of the mineral requirements of *P. neriifolia* seedlings showed that the primary growth response of seedlings was to increasing levels of applied ammonium nitrogen. An upper limit of applied ammonium nitrogen of between 4 and 7 mM applied as 60 ml per week was identified. At these levels of applied ammonium nitrogen, seedling growth also responded to applied phosphorus and potassium. These latter responses occurred at phosphorus (0.65 mM) and potassium (1.25 mM) concentrations considerably higher than previously reported for other species of Proteaceae.

Shrub architecture and biomass accumulation of mature *P. neriifolia* shrubs exhibited both age and nutrient related changes. Vegetative and reproductive growth increased with increasing shrub age and also in response to the application of inorganic fertilizers. Changes in biomass allocation patterns were primarily nutrient related. In unfertilized shrubs, there was greater allocation of resources to below-ground biomass, a strategy common in plants growing on nutrient poor soils. Vegetative shoot growth did show decreasing stem lengths with increasing age of the shrubs. This was, however, alleviated by the application of inorganic fertilizers. There were also significant increases in the number of flowers produced, both as a result of increasing shrub age, and thus size, and as a result of applied nutrients. Larger flowers were produced in response to inorganic fertilization.

Two models have been proposed to describe the timing of growth events of over-storey plants on nutrient-limited soils. The phenology of *P. neriifolia* did not conform to predictions of either model and shifts in phenophase events could not be explained. Although shrub phenology is nutrient related, the application of inorganic fertilizers did not affect the timing of growth events. Further, the phenology of the *P. neriifolia* shrubs did not change with increasing age of the shrubs. Seasonal variation in the occurrence of proteoid roots was observed, and the influence of soil moisture and ambient temperature in this and other shrub seasonality was shown to be important. However, the study of soil moisture influences were hampered by the plastic mulch used in the cultivation process. The synchronous nature of phenological events, for example, maximum litter production and maximum proteoid root occurrence immediately prior to peak vegetative growth, were highlighted. The slow decomposition of leaf litter and the resultant increase in litter below shrubs was also noted.

Seasonal variations in the availability of soil nutrients were found. However, periods of highest availability could not be linked to periods of peak shrub growth. Hence, peak nutrient concentrations in shrub components did not follow periods of highest nutrient availability in the soil.

Seasonal variations in nutrient concentration of shrub components were found and, in general, highest leaf and stem concentration was found during periods of peak vegetative growth, and highest flower component nutrient concentrations were found at time of flower bud set. Shrub age and the addition of inorganic fertilizers did result in changes in shrub component nutrient concentrations. Nitrogen, phosphorus and potassium concentrations in seven year old shrubs were higher than in unfertilized ten year old shrubs and higher than in ten year old shrubs fertilized with Plantosan plus urea. Nutrient concentrations in ten year old shrubs fertilized with Plantosan plus ammonium sulphate were comparable with those in seven year old shrubs. This shows, therefore, that the growth of unfertilized shrubs and shrubs fertilized with Plantosan plus urea, was at the expense of previously absorbed nutrients. Since the available nutrient levels of soils of unfertilized shrubs did show depletion with time, this would explain the lower absorption of nutrients by these shrubs. However, soils which were fertilized with either Plantosan plus urea or Plantosan plus ammonium sulphate showed an increase in both soluble and total nitrogen and available phosphorus levels. This increase in plant nitrogen levels under Plantosan plus ammonium sulphate suggests that nitrogen in the urea form is not as readily utilized by *P. neriifolia* as nitrogen in the ammonium form. Hence, shrubs fertilized with Plantosan plus urea also grew at the expense of previously absorbed nutrients.

While maximum nutrient uptake by the shrubs was linked to the highest occurrence of proteoid roots, this occurred during the season of lowest rainfall. However, the influence of the plastic mulch in maintaining a relatively constant soil moisture was highlighted. This constant soil moisture thus facilitated nutrient uptake during the season of lowest rainfall.

Nutrient budgets for *P. neriifolia* cultivated in a summer rainfall area were shown to be complex but efficient. Nutrient inputs from rainfall and the soil are low but higher than the loss of nutrients through stream-water. Further, despite slow rates of litter decomposition, nutrients are cycled through shrub litter. This litter cycle was shown to be particularly important in shrubs growing on nutrient-poor soils. Therefore, in the absence of flower harvesting, nutrient inputs, cycling and internal nutrient redistribution are sufficient for the continued growth of the shrubs. However, the removal of flowers for commercial sale results in large losses of nutrients from the shrubs. These losses cannot be made up by inputs or cycling and continued shrub growth was shown to occur at the expense of previously absorbed nutrients. Such a scenario is not sustainable and nutrient inputs external to the system were required. In this investigation, additional inputs were supplied in the form of two inorganic fertilizer preparations, Plantosan plus ammonium sulphate and Plantosan plus urea. Nutrient budget deficits were redressed through fertilization with Plantosan plus ammonium sulphate but not with Plantosan plus urea. This further suggests that *P. neriifolia* is better able to utilize nitrogen in the ammonium form than in the urea form. Although cultivated *P. neriifolia* shrubs responded to ammonium nitrogen fertilization, there was evidence that shrubs were phosphorus limited and that phosphorus in the inorganic fertilizers was also responsible for increased growth. Shrub responses to potassium were complex and potassium budget deficits, even under conditions of potassium fertilization, indicate that the potassium concentration in the inorganic fertilizer preparations tested in this investigation was too low, and that higher levels of applied potassium might be required.

6.7 Horticultural implications

It has been repeatedly stressed throughout this thesis that studies were not designed to provide definitive fertilizer application information for Proteaceae under cultivation. However, certain aspects of the work presented do have horticultural implications and the thesis would be incomplete if these were not highlighted.

- As recommended for other Proteaceae, for example, Dennis and Prasad (1986), it is likely that above- and below-ground plant growth of *P. neriifolia* seedlings and cuttings grown in the nursery prior to planting out in the field, will respond favourably to the application of inorganic fertilizers based on the optimum treatment in this study viz. nitrogen, phosphorus and potassium at 7; 0.65 and 1.25 mM, respectively, applied at a rate of 60 ml per week.

- Since nutrient loss through the harvest of flowers for commercial sale is higher than previously thought (Claassens, 1986; Low and Lamont, 1986) it is likely that field cultivated shrubs will benefit from the application of low levels of fertilizers. Low levels of application are particularly true for phosphorus and potassium fertilization, while it is likely that cultivated *P. neriifolia* shrubs will respond favourably to relatively high levels of nitrogen fertilization, particularly in the ammonium form. This is in accordance with results from other studies and it is likely that nitrogen in the nitrate form should be avoided (Claassens, 1981; Nichols and Beardsell, 1981; Vogts, 1982; Heinsohn, 1983). In Proteaceae cultivated for the harvest of flowers for commercial sale, applications of inorganic fertilizers have been shown to affect whole shrub growth, flower production, and size favourably.

- Results from studies on the timing of shoot growth and flower production in *P. neriifolia* cultivated in a summer rainfall area can be used in improving bush productivity through pruning. The harvest of flowers can be regarded as the first stage of pruning. Although lateral shoots may also be removed during flower harvest, flower harvest does remove apical dominance of the flower allowing for further lateral shoot production. A second pruning of dead and diseased vegetative and floral shoots should follow immediately at the end of the reproductive cycle viz. July, to encourage further lateral shoot production. This second pruning must be completed by the end of July to take maximum advantage of the optimum growth period beginning late July/early August. During this period the lateral shoots will grow, become primary and produce flowers. This is in accordance with Brits, Jacobs and Steenkamp (1986) who suggest that this second pruning operation should be completed before new vegetative shoots have grown too much. Controlled pruning in this manner, taking advantage of all growth periods, could increase cut-flower yields and the productive life of cultivated plants in summer rainfall areas.

- As recommended by Lamont (1986) there should be no cultivation in the immediate area of protea shrubs as this could adversely affect the growth of proteoid roots. Further, litter that has accumulated beneath the shrubs should be left in place as it is in this layer that much proteoid root growth occurs (Lamont, 1986). Also, the litter layer is an important source of nutrients in the nutrient cycling regime of the shrubs.

- Lastly, the *P. neriifolia* cultivated in this investigation were grown with the aid of plastic mulch. While the mulch does serve adequately for the retention of comparable soil moistures throughout the year, it does have certain practical constraints. Litter fall is onto the mulch and unless the mulch breaks up due to deterioration, proteoid roots are excluded from this litter layer. Furthermore, the plastic mulch does make fertilizer applications difficult and it is likely that a percentage of nutrients applied in this investigation did not reach the root layer as intended. However, if shrubs are cultivated without plastic mulch some form of irrigation would be necessary particularly for the dry winter period. This is because proteoid root growth, nutrient absorption, and shoot growth all show a peak in late winter/early spring, and the lack of soil moisture during this period could be growth limiting. This would depend on whether shrubs are water or nutrient limited.

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