THE EFFECT OF ENVIRONMENTAL FACTORS AND CROP INTERFERENCE ON THE BIOLOGY OF YARROW (*Achillea millefolium* L.) SEED AND SEEDLINGS

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by

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I dedicate this thesis to my wife
Ratnaseeli and my daughter Sakunthala.

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A population of 58 seedling yarrow (*Achillea millefolium*) plants m^{-2} produced approximately 243,000 viable seeds per square metre in the first season of growth and development. Approximately 10% of the freshly harvested yarrow seed had no dormancy and was able to germinate in the presence of adequate amounts of water and ambient conditions of temperature and aeration suitable for normal vegetative growth and development. The rest of the imbibed seed required direct light for complete germination. Even in the absence of light, 30% to 50% of these dormant seeds germinated when scarified and/or stratified or when supplied with 10^{-3}M KNO_3 solution or when subjected to diurnal alternation of temperature of 20° - 30°C. It is evident that at least five conditionally dormant types of seed are present in yarrow.

When adequate moisture was available the yarrow seed lying on the soil surface germinated and established seedling plants in the spring, summer and autumn months. However, when the seeds were buried in the soil a substantial proportion of them did not germinate due to the lack of the special environmental cues required to break dormancy. They remained viable for varying lengths of time depending on the depth at which they

were buried in the soil profile. Approximately 50% to 60% of the seed buried at 16 cm and 32 cm, respectively, remained viable after 2 years while only ≤ 10% of the seed buried at 8 cm or less were viable after the same period of time. The viable seed germinated when subsequently exposed to light.

It is suggested that the above detailed characteristics of the yarrow seeds are of ecological importance as they would undoubtedly ensure that the seeds germinate close to the soil surface in land relatively free of other vegetation and the ambient conditions present at the time of seed germination would be suitable for the normal growth and development of the emerging seedlings.

The reduction of light availability to seedling yarrow plants markedly suppressed their growth and development and indicated that it was essentially an obligatory 'sun' species. However, established yarrow seedlings survived in 6.4% daylight and their total reproductive effort, at this light intensity, was directed towards rhizome production. Similar trends in vegetative growth and development and the reproductive effort were observed when seedling yarrow stands were grown in association with barley (*Hordeum vulgare*) or pea (*Pisum sativum*) crops. Although the aggressivity of seedling yarrow grown with barley or pea plants was low during the early phase of vegetative growth and development, the yarrow in association with the pea plants exhibited markedly better growth and development compared to when grown with the barley plants. Both crop species shaded the yarrow plants grown with them and also obtained a greater share of the available soil N, P and K. In addition to this, the barley roots appeared to exert an allelopathic influence on the neighbouring yarrow plants which was deleterious to yarrow growth. The greater penetration of light through the pea canopy and the absence of allelopathic interference by the pea plants were important factors contributing to the

comparatively better growth and development of seedling yarrow plants associated with this crop species.

When seedling yarrow plants were grown with barley or pea plants, root interference between them commenced earlier than shoot interference. In the yarrow/barley association root interference continued to be of greater importance than shoot interference in suppressing the growth of the former species during the early stages of vegetative growth. The converse was true in the yarrow/pea plant association.

The yarrow plants present in the barley or pea crops grew rapidly once the crops were harvested with rhizome development being a major contributor to the increased growth.

The characteristics of the yarrow seeds and seedlings helped explain the persistance of the species in arable land while the markedly better growth and development of the yarrow seedlings in association with the pea crop showed that it was an opportunistic weed. The usefulness of the current knowledge of the biology of yarrow in planning and executing various mechanical and cultural practices aimed at controlling the species on arable land are detailed and areas of further study are suggested.

CONTENTS

CHAPTER PAGE

CHAPTER PAGE

CHAPTER PAGE

CHAPTER PAGE

CHAPTER PAGE

LIST OF FIGURES

LIST OF TABLES

PREFACE

Within the scope of the work presented in this thesis are the dormancy, germination and survival characteristics of yarrow seed; the responses of seedling yarrow to shading and crop interference; and the nature of interference between seedling yarrow and barley or pea plants. The aspects chosen for study were those considered likely to reveal information that could be used in developing suitable strategies for controlling seedling yarrow infestations on arable land.

The thesis begins with an introduction to yarrow with special emphasis on the work done in New Zealand (Chapter 1). Each of the following four chapters (Chapters 2, 3, 4 and 5) have their own literature review and detail experimental work on seed dormancy and germination and the longevity of yarrow seed in the soil at different depths (Chapter 2); effect of different levels of shade on the survival, dry matter accumulation and reproductive effort of seedling yarrow plants (Chapter 3); the growth and development of seedling yarrow in a pure stand and in association with a barley crop or a pea crop and its performance after the crops were harvested (Chapter 4); and the nature of interference between seedling yarrow and barley plants or pea plants and the aggressivity of the seedling yarrow grown in association with either of the latter two species (Chapter 5). In the final chapter (Chapter 6), the experimental results are discussed more generally, taking into account the characteristics of persistance and competitive ability of seedling yarrow and their significance in the control of the species on arable land.

The mean data used in the drawing of figures presented in this thesis are tabulated in the appendices and an outline of the growth analysis technique employed in Chapter 4 is addended. Some developmental stages of seedling yarrow grown in pure stand are shown in Appendix 13. The life

history of seedling yarrow is given in Appendix 15. An appendix on the climatological data during the experimental period is also addended (Appendix 1).

CHAPTER 1

AN INTRODUCTION TO *Achillea millefolium* L.

Detailed and comprehensive literature reviews on *Achillea millefolium* L. have been recently published by Bourdôt (1980) and Warwick and Black (1982). In this chapter, a general introduction to the *Achillea millefolium* complex is given with special reference to some aspects of research work carried out in New Zealand. Other work related to the specific experiments carried out by the author are referred to in the appropriate chapters that follow.

1.1 CLASSIFICATION

Achillea millefolium L., a perennial rhizomatous herb, belongs to the family Asteraceae (Compositae) and is a member of the tribe Anthemidae. This tribe has 8% of the total number of genera and 13% of the species of the family (Heywood and Humphries, 1977). They reported that the haploid chromosome number of the *Achillea* genus is 9(n = 9), while diploid, tetraploid, hexaploid, octaploid and decaploid plant species were present in this genus.

Chromosome counts on the *Achillea millefolium* L. plants growing close to the research fields at Lincoln College, New Zealand, revealed that they were hexaploids (Bourdôt, 1980). All experiments reported in this thesis were carried out using sexual reproductive propagules collected from plants growing in the same area. The reproductive propagule will be hereafter referred to as a seed, but is described more accurately as a single seeded dry indehiscent fruit or achene (Bostock, 1978).

1.2 NOMENCLATURE

Gray (1950) reported that the genus *Achillea* was named after Achilles, who is credited with having discovered the plant's healing powers, while the species name was given in reference to the finely dissected nature of the leaves. *Achillea millefolium* L. is referred to as yarrow and milfoil in many countries (Korsmo, 1954). The plant is commonly referred to as yarrow in New Zealand (Standard Common Names for Weeds in New Zealand, 1969).

1.3 GEOGRAPHICAL DISTRIBUTION

Holm, Pancho, Herberger and Plucknett (1979) reported that while yarrow is not a serious weed in any country, it is a principle weed in Finland, Norway, New Zealand and Sweden. It has been reported as a common weed in Argentina, Australia, Canada, England, Germany, Hawaii, Iran, Soviet Union, Spain, and North America, while in India and Chile it is present, but its rank of importance as a weed is not known. In Afghanistan, Alaska, and Poland, yarrow has been reported to be a part of the native flora.

1.4 HABITAT

In New Zealand, yarrow grows well from the drier and warmer environments of Canterbury (mean annual rainfall and temperature of 600 - 800 mm and 10 - 12.5^{o}C) to the wetter environments in Southland (mean annual rainfall and temperature of 800 - 1200 mm and 7.5 - 10^{o}C) (Bourdôt, 1980). It is present on different soil types and is widely distributed on lighter soils, where water stress is common in summer (Matthews, 1976). Its drought-resistant characteristics have also been reported by Reynolds (1961).

Yarrow is present in pastures (Fenner, 1978), lawns (Levy, 1931), roadsides, and wastelands (Clapham, Tutin and Warburg, 1962; Matthews, 1975) and is well adapted to habitats that are constantly disturbed, such as land under cereals (Hilgendorf and Calder, 1952); peas (*Pisum sativum*), beans (*Phaseolus vulgaris*), beet (*Beta vulgaris*), and seed crops of white clover (*Trifolium repens*) (Bourdôt, White and Field, 1979; Bourdôt and Butler, 1981).

1.5 WEEDINESS

Yarrow was introduced to New Zealand from Europe as a component of pasture mixtures, and was found to be highly palatable to sheep (Cockayne, 1920; Reynolds, 1961). It has since emerged as a problem weed in arable lands owing to the decline in fallowing in mixed cropped lands (Hilgendorf and Calder, 1952); the ability of yarrow to withstand prolonged and severe grazing and conventional tillage of the soil; its ability to survive under competition from vigorously growing species (Reynolds, 1961); the production and growth of rhizomes in the mild winter periods experienced in New Zealand (Bourdôt, 1980); lack of suitable herbicides for control (Matthews, 1975), and probably due to the dormancy and survival characteristics of its seeds. It is not a weed of importance in well managed pastures, and develops dominance only when the sward is damaged by herbicides, insect attack, prolonged dry weather and/or stock activity (Matthews, 1976).

1.6 USEFULNESS OF YARROW

Yarrow is of limited use in New Zealand. It is favoured for lawns and playing areas which are subjected to heavy wear. Its mat-forming rhizome system and the arrangement of leaves in prostrate rosette-like fashion gives a dense and even stand which requires little or no mowing (Reynolds, 1961). He stated that in the early days of pasture establish-

ment a little yarrow seed was sown in the hill country lands, especially in steeper and drier areas, after bush burning. With the advent of fertilizer top dressing, use of improved cultural practices, and the introduction of more productive species, the importance of yarrow has diminished. Its intentional establishment is no longer encouraged. However, naturally established yarrow remains a rich source of food for sheep and deer (Warwick and Black, 1982) and is considered to have valuable pharmaceutical properties (Chandler, Hooper and Harvey, 1982).

1.7 DEVELOPMENTAL STAGES

Bourdôt, White and Field (1979) reported that large quantities of freshly shed seed germinated with the autumn rains (April - May) and the seedlings over-wintered as rosettes (June - August). With the onset of spring, these seedlings initiated rhizomes. From late spring to early autumn (November to March) rhizome production, flower stem elongation, flowering, seed set, seed maturity, and seed shedding occurred. The shedding of seed continued during late autumn - early winter, but these did not germinate until the following spring (Bourdôt, 1980).

The autumn-emerging seedlings were often ploughed into the soil during early spring cultivation (Kannangara, unpublished) and apart from the new plants that established from fragmented rhizomes, spring germinating seedlings were observed to grow in association with a range of crops.

The developmental stages of the spring-emerging shoots from fragmented rhizomes have been studied by Bourdôt (1980). There is no reported work on the growth and development of spring-emerging seedlings.

1.8 REPRODUCTION AND DISPERSAL

Knuth (1908) reported that if cross pollination of the disc florets of yarrow failed, they were able to undergo selfing, while Weijer (1952)

stated that absolute self-sterility existed in yarrow. In Canterbury, the author has observed honey bees (*Apis milliflora*) as regular visitors to yarrow flowers. A number of Coleopterans, Dipterans, and Lepidopterans have been reported as insect visitors to yarrow inflorescences (Knuth, 1908).

Bourdôt, White and Field (1979) found that in a natural stand of yarrow growing in Canterbury, the first ray florets appeared in late December and flowering continued until mid-January. They recorded the seed yield components and estimated that 900,000 seeds m^{-2} were produced. This estimate was made on a population of plants growing from rhizomes. Single seedling plants growing without interference from neighbouring plants produced approximately 60,000 seeds during the first season of flowering (Bourdôt *et al.*, 1979). No published work is available on seed production of a seedling population of yarrow.

The seed has no pappus and is wedge-shaped in outline. Bostock (1978) considered these seeds to have poor aerodynamic efficiency and thus to be shed close to the parent plant. Owing to the small size and light weight of the seeds, they were found to be wind blown for short distances while wider dispersal may occur by their entanglement in sheeps' wool (Reynolds, 1961).

Korsmo (1954), describing the anatomy of yarrow, noted that apart from sexual reproduction, this plant was able to multiply vegetatively. He reported that the organs of vegetative multiplication were branched rhizomes which lay shallow in the soil. The growth of these rhizomes help the plant to spread laterally; Salisbury (1942) stated that they extend 7 to 20 cm $year^{-1}$. In New Zealand, the reproductive potential of the rhizomes in arable lands has been briefly referred to by Saxby (1944), Hilgendorf and Calder (1952), and Reynolds (1961). In more detailed studies on the biology of the rhizomes in arable lands, Bourdôt (1980) found that

axillary buds on intact rhizomes attached to the parent plant remained dormant due to apical dominance. Once this effect was negated by damage to the apical bud or by fragmentation, some of the buds on the rhizomes sprouted and grew vertically upward to form aerial shoots. The buds that did not sprout owing to the apical dominance imposed on them by the shoots that were already growing, did so when the rhizome pieces were further fragmented and/or the shoots on them were damaged. When the shoots formed from vegetative buds had 5 to 6 leaves, they initiated rhizomes. Bourdôt (1980) found that there was a six-fold increase in rhizome weight of plants over the winter period in Canterbury, New Zealand.

The rhizomes are very brittle (Hilgendorf and Calder, 1952) and are easily fragmented during cultivation of the land. These fragments may be dispersed by implements used for cultivation. There is no reported work on the extent of such dispersal and the resulting yarrow infestations of different fields.

Many workers have shown the importance of knowing the biology of weeds if they are to be efficiently managed and thus prevented from causing economic damage to crops (Chancellor, 1968, 1970; Cussans, 1970; Harper, 1977). Where yarrow is a problem weed on arable lands, farmers have realized that the potential damage to crops from seedling plants of the weed was greater than from their rhizomatous plants. This is mainly owing to the difficulties involved in predicting the density of seedling yarrow infestations that may occur in crops and the lack of suitable post-emergence 'control' measures for this weed. However, there is a critical lack of experimental evidence on the biology of seed and seedling yarrow in arable lands. The experimental work carried out in the present study was undertaken to correct this anomaly and thus pave the way for the logical and efficient use of agronomic practices in managing this weed.

CHAPTER 2

DORMANCY, GERMINATION, AND LONGEVITY OF VIABILITY OF YARROW SEED

2.1 INTRODUCTION

2.1.1 Dormancy and Germination

Some angiospermous seeds are capable of germinating immediately after they are shed (e.g., *Phaseolus vulgaris* and *Pisum sativum*) while others require special environmental cues (e.g. *Lactuca sativa* c.v. Grand Rapids, *Taraxacum officinale* and *Cirsium arvense*) and/or periods of after-ripening (e.g. *Betula lenta, Polygonum lapathifolium* and *Prunus persica*) before they can germinate. The former seeds are in a quiescent state, while the latter are in a state of dormancy (Amen, 1968; Villiers, 1975). Some seeds which are shed in a quiescent state, and thus able to germinate after a brief period of exposure to an adequate supply of water in the presence of suitable temperature and aeration, may acquire dormancy (e.g. *Ambrosia trifida* and *Xanthium* spp.) at a later stage if they experience unfavourable ambient conditions (Harper, 1957).

Almost all habitats in which higher plants grow are subjected to environmental stresses. One decisive way in which plant species successfully escape these adverse effects and ensure their continued survival is by the production of dormant seeds. Thus, seed dormancy is an adaptive mechanism in plants that allows them to tide over untenable stress conditions and take advantage of favourable environmental niches at other times. In annuals, biennials and some perennials which are totally dependent on seeds for the continuity of the species, seed dormancy mechanisms play a vital role; in other perennials with vegetative modes of reproduction, the production of dormant seeds is an additional means of ensuring survival

of the species (Harper, 1957).

Environmental conditions prevailing during the growth of plants, especially during seed maturity, affect the degree and nature of innate dormancy of seeds (Koller, 1962; Popay and Roberts, 1970; Gutterman, 1973). This may explain some of the variation observed in the germination of seeds from the same species as well as seeds from the same plant (Harper, 1957; Frankland, 1976). Differences in the genetic composition of seeds may also be responsible for this variation (Wittington, 1973). Villiers (1975) attributed the main causes of seed dormancy to the nature of the seed coat, morphological and physiological state of the embryo, and the presence of various physiological inhibitors.

In some species (e.g., *Trifolium repens*, *Xanthium* spp., and *Betula pubescens*) dormancy due to the physical and mechanical nature of the seed coat (hard coated seed) may be brought about by impediments to the movement of water (Hyde, 1954; Taylor and Hendricks, 1977) and gases (Black, 1959; Come and Tissaoui, 1973) to the embryo, offering mechanical resistance to the expansion of the embryo (Esashi and Leopold, 1968), and by varying the amount and quality of light received by the embryo (Ballard, 1973). One or more of these characteristics of the seed coat can maintain the seed in a dormant state. In other plant species, seed dormancy is caused by morphological and physiological immaturity of the embryo (Amen, 1968; Nikolaeva, 1977). Seeds with morphologically immature embryos (e.g., *Polygonum* spp., *Prunus cerasus*, and *Heracleum sphondylium*) require a period of after-ripening for further development and maturity of the embryo (Stokes, 1952). In certain species (e.g. *Taraxacum officinale* and *Circium arvense*), low concentrations of hormones and enzymes and the presence of inhibitors that block metabolic pathways, or both, are responsible for dormancy in seeds with physiologically immature embryos (Mayer and Poljakoff-Mayber, 1975). Inhibitors, especially compounds such as coumarin

(Evanari, 1949) and abscisic acid (Lewak and Rudniki, 1977) have been implicated for dormancy characteristics exhibited by some seeds. The concept that inhibitors cause seed dormancy gained credibility when it was shown that leaching was able to induce some dormant seeds to germinate (Wareing and Foda, 1957; Villiers and Wareing, 1965). More recently, Khan (1977) has suggested that the presence of physiologically effective levels of inhibitors and promoters of germination were more important than the actual amounts of them, in determining whether a seed is dormant or not. Though the nature of the seed coat, state of maturity of the embryo, and the presence of inhibitors have been discussed as separate factors responsible for seed dormancy, a combination of these factors is usually involved (Mayer and Poljakoff-Mayber, 1975; Villiers, 1975).

Dormant seeds present on the soil surface or those buried to various depths in the soil may be subjected to scarification (Harper, 1977; Nikolaeva, 1977); stratification (Amen, 1966; Vincent and Roberts, 1977); varying light regimes, alternations of temperature, and different concentrations of soil solutes (Vincent and Roberts, 1977); and leaching (Harper, 1977). Depending on the nature of seed dormancy and the ambient conditions to which these seeds are exposed, the loss of dormancy occurs over varying lengths of time. The interaction of two or more of the above detailed factors to which seeds in the soil may be exposed have been shown to break their dormancy (Steinbauer and Grigsby, 1957; Thompson, Grime and Mason, 1977; Vincent and Roberts, 1977; 1979).

Scarification of hard coated seeds induces them to germinate by increasing the permeability to water and gases (Thornton, 1935) and by weakening the mechanically resistant seed coat. If the seed coat cracks during scarification it allows unimpeded movement of solutes into and out of the seed. If pieces of the seed coat become detached from the seed, it may be equivalent to physically removing inhibitors. Scarification may also lead to increased sensitivity of the seed to light and temperature;

cause metabolic changes in the living tissues damaged during scarification (Mayer and Poljakoff-Mayber, 1975; Khan, 1977) and lead to oxidation of inhibitors in the seed (Wareing and Foda, 1957; Porter and Wareing, 1974). It is possible that any one of these actions or a combination of them may be responsible for the loss of dormancy in hard coated seeds.

After-ripening of seeds with immature embryos can occur either when they are subjected, in the imbibed state, to temperatures ranging from 1 to 10°C for a few weeks or by storing them in the dry state at a temperature between 15 to 20°C for a period ranging from some months to several years (Stokes, 1965). In the field, buried seeds are often in an imbibed state and thus cold temperature stratification is likely to occur, especially during the winter period. In seeds with morphologically immature embryos, cold stratification promotes embryo growth; such changes have been reported in *Prunus cerasus* (Pollock and Olney, 1959) where at 5°C the embryo axis increased in cell number, dry weight and total length. In *Heracleum sphondylium,* a close correlation between embryo growth and loss of stored materials from the endosperm (Stokes, 1952) suggested that low temperature stratification may be stimulating efficient transfer of nutrients from the endosperm to the embryo, thereby promoting embryo growth. Low temperature stratification is also known to change the levels of germination inhibitors and promotors as well as the metabolism of dormant seeds (Mayer and Poljakoff-Mayber, 1975; Lewak and Rudnicki, 1977). Abscisic acid, a well-known inhibitor which is closely related to embryonic dormancy (Lewak and Rudnicki, 1977) decreased when dormant seeds of some plant species were subjected to cold temperature (Villiers and Wareing, 1965; Taylorson and Hendricks, 1977), leading to an increase in germination. Many other inhibitors may also be affected in a similar way. Cold stratification of dormant seeds has been reported to increase the levels of germination promotors like gibberellic acid (Frankland and Wareing, 1966) and cytokinins (Webb, Van

Staden, and Wareing, 1973). Therefore, it appears that when dormant seeds, requiring cold stratification to break dormancy, are chilled the hormonal equilibrium is changed from the dominance of inhibitors to the dominance of promoters. Changes in the metabolism of some dormant seeds have been observed to occur with low temperature stratification (Stokes, 1953; LaCroix and Jaswal, 1973), although it is not clear whether these changes are primarily responsible for release of seeds from dormancy or occur as a consequence of this process (Mayer and Poljakoff-Mayber, 1975).

The influence of light on germination has been known for a long time. Some seeds (e.g., *Cynodon dactylon, Festuca* spp. and *Sorghum halepense*) require light for germiantion (positively photoblastic). Other seeds (e.g., *Atriplex dimorphostegia* and *Phacelia* spp.) do not germinate in the presence of light (negatively photoblastic) (Evanari, 1965) while there are seeds (e.g., *Oryza sativa, Pisum sativum, Lolium perenne*, and *Trifolium repens*) which are indifferent to the presence or absence of light and germinate in both situations (Mayer and Poljakoff-Mayber, 1975). Red light (R) promoted germination while far-red light (FR) inhibited it in positively photoblastic seeds (Toole, Borthwick, Hendricks, and Toole, 1953). Some negatively photoblastic seeds also responded to R and FR light in a similar way (Evanari, 1965). Photochrome was identified as the substance responsible for the differential response to R and FR light (Butler, Norris, Siegelman, and Hendricks, 1959) and is present in two principal interconvertible forms; the active form (P_{fr}) which promotes germination and the inactive form (P_r) which inhibits germination (Villiers, 1972). The total amount of phytochrome in seeds of different species as well as among the seeds of the same species, varies. Arising from this difference, the number of molecules of P_{fr} that are needed by seeds to induce germination also varies (Frankland, 1976). The mechanism of action of P_{fr} in bringing about germination is still not clear (Mayer and

Poljakoff-Mayber, 1975) though it has been suggested that phytochrome acts on the cell membrane either to release germination promoters or to activate genes that lead to the production of promoters. Villiers (1975) postulated that P_{fr} induces the embryo to produce cytokinins and gibberellins; the cytokinins neutralizing the inhibitors present in the seeds, while gibberellin induces the production of hydrolytic enzymes which in turn act on the stored seed reserves.

The alternation of temperature alone can cause a certain proportion of positively photoblastic seeds to germinate (Thompson, 1974). This has been observed in many species, including *Achillea millefolium* (Robocker, 1977; Bostock, 1978) and *Taraxacum officinale* (Bostock, 1978). It has been suggested that the acceleration of rehydration and synthesis of phytochrome during the higher temperature phase and the deceleration of the reversion of P_{fr} to the P_r form during the lower temperature phase of the alternating temperature cycle maintains the P_{fr} level at a physiologically effective level, thereby inducing germination of dormant seeds (Toole, 1973). The variations in phytochrome and inhibitor levels in seeds may be responsible for a certain proportion of seeds being able to germinate while others continue to be in a dormant state.

Many substituted phenylureas and thioureas, other nitrogen-containing compounds including nitrites and nitrates, ethylene-generating compounds, and some chelating compounds are known to have germination promotion effects on dormant seeds (Thomas, 1977). Out of these, nitrate has been recognised as a major dormancy-breaking agent for many seed species, including *Phytolacca americana, Astrebla lappacea,* and *Ricinus communis* (Toole, Hendricks, Borthwick and Toole, 1956; Steinbauer and Grigsby, 1957; I.S.T.A., 1976). In *Achillea millefolium* (yarrow), nitrate was found to induce a certain proportion of seeds to germinate in the dark (Bostock, 1978). Little is known of the mechanism involved in dormancy breaking by nitrate compounds, though it has been suggested that it leads to an increase in seed cytokinins

(Thomas, 1977).

2.1.2 Longevity of Seed Viability

Seeds of many plant species, including *Nelumbo nucifera, Lupinus articus, Chenopodium album,* and *Spergula arvensis* have been found to remain viable for long periods of time when buried in the soil under natural conditions (Justice, 1973). Irreversible changes in metabolism (Anderson, 1973) and ultra-structure (Koostra, 1973) occur in imbibed seeds when they are stored. It is possible that similar changes occur in seeds which are buried in the soil, thus leading to a decrease in their survival capacity.

Perhaps the best known studies on the longevity of viability of buried seeds in undisturbed soil were initiated by Beal (Kivilaan and Bandurski, 1973) and Duvel (Toole, 1946). In Beal's study, after 90 years of burial, some *Verbascum blattaria* seeds were still viable. In Duvel's experiment, after 39 years of burial, 36 of the original 107 species still had viable seeds. In a more recent study, Lewis (1973) found that *Chenopodium album, Ranunculus repens,* and *Rumex crispus* seeds remained viable for at least 20 years when buried in the soil. These findings indicate that seeds of weeds and wild plants survive for long periods when buried in the soil. Seeds of some species show low survival when buried in soil, and this is mainly due to their germination *in situ* (Evans, 1960; Schafer and Chilcote, 1970). Many workers have found that increasing soil depths favour greater seed longevity (e.g., Toole, 1946; Rampton and Ching, 1966; Dawson and Bruns, 1975). Low, stable temperatures at the deeper soil depths (Turner, 1933); lack of aeration in waterlogged soils (Lewis, 1961); increasingly low oxygen and high carbon dioxide levels down the soil profile (Bibbey, 1948) have been suggested as possible reasons for the longer survival of seeds in the deeper soil layers.

2.1.3 Ecotypes of Yarrow

Achillea millefolium complex occupies a diversity of altitudinal and latitudinal climates (Clausen, Keck and Hiesey, 1958) and is known to have developed an exceptional number of ecotypes. It is a problem weed in the arable lands in the Canterbury Plains in New Zealand (Bourdôt, White and Field, 1979). It is possible that the ecotype(s) present in this region have quite different biological characteristics to those found in other countries. No detailed study has been made to identify the presence of ecotypes in New Zealand, though Bourdôt (1980), quoting Given, mentions the possibility of the existance of such types. The experiments reported in this chapter were carried out to establish the seed dormancy, germination and survival characteristics of *Achillea millefolium* commonly present in the Canterbury Plains in New Zealand.

2.2 EXPERIMENTAL RESULTS

Experiment 1: Effect of Light, Temperature and Moistening Agent on the Germination of Yarrow Seed

2.2.1 Materials and Methods

2.2.1.1 Seed Material

Sun-dried seed heads were collected on 3 March 1979 from a naturally growing population of yarrow found close to the research fields at Lincoln College. They were gently rubbed on a sieve to dislodge the seeds and the chaff and light seeds were removed by blowing air through the mixture at a constant velocity. Laboratory germination tests were carried out on samples of these cleaned seeds, according to the recommendations of I.S.T.A. (1976). The seeds were imbibed in water and subjected to 20 - 30^{o}C alternation of temperature with 8 hours light day^{-1} (3875 Lux intensity);

98% (SE 2%) germination was obtained after 28 days incubation. The cleaned seed was immediately used in the experiment.

2.2.1.2 Experimental Design

A completely randomised factorially designed experiment with 2 light treatments (complete darkness and 8 h light day^{-1}), 3 temperatures ($20^{o}C$, $30^{o}C$ and alternating 20 - $30^{o}C$) and 2 moistening agents (water and $10^{-3}M$ potassium nitrate solution) was carried out to evaluate their effects on the germination of freshly harvested yarrow seed. Each treatment was replicated 6 times, with 100 yarrow seeds per replicate treatment.

2.2.1.3 Experimental Procedure

Each of three growth chambers was regulated to supply 8 hours light and 16 hours dark day^{-1}; the light was given from 8 Phillips 80 watt cool white fluorescent tubes (TL33) and 6, 60 watt incandescent strip lights, giving a light intensity of 3875 lux at the surface of the tray on which the petri dishes containing the yarrow seeds were kept (measured by a 'Light-Master Photometer' manufactured by Evans Electroselenium Ltd, Essex). The source of light was from the top of each growth chamber and was placed about 1.5 m above the seeds; the growth chambers were lined with aluminized Mylar reflector foil. The three separate growth chambers were set at either constant temperatures of $20^{o}C$ and $30^{o}C$ or at 20 - $30^{o}C$ alternating temperatures, respectively; the period of higher temperature in the alternating temperature treatment coincided with the light period.

On 3 March 1979, glass petri dishes were lined with Whatman grade 181 9 cm germination pads and 100 yarrow seeds were placed in each dish; 6 ml of distilled water or a solution of $10^{-3}M$ potassium nitrate (KNO_3) was added into the appropriate dishes and covered with their lids. The treatments to be subjected to complete darkness were immediately transferred into individual black polythene bags and those intended to receive light were placed in individual clear polythene bags. In addition to

supplying the appropriate light environment, these bags prevented the loss of moisture from the petri dishes.

Depending on the treatment, the seeds in the petri dishes were transferred into the appropriate growth chambers and incubated for 28 days (until 31 March 1979) before germination counts were made. The seedling plants and seeds with emerged radicles that were 1 mm in length or more were counted as germinated and removed from the petri dishes.

2.2.2 Results

The main effects of temperature, moistening agent, light, and the interactions of temperature x light and moistening agent x light were significant (Tables 2.1, 2.2), while there were no significant interactions of temperature x moistening agent and temperature x moistening agent x light. All ungerminated seeds were incubated in conditions recommended by I.S.T.A. (1976) for obtaining maximum germination (refer section 2.2) for a further 14 days. Except for one or two seeds, all others germinated. This suggests that they were viable but did not germinate previously owing to the imposed effects of the treatment.

2.2.2.1 Effect of Temperature and Light

The germination of yarrow seeds in continuous dark at constant temperatures of 20°C and 30°C or in alternating temperatures of 20 - 30°C was significantly lower than when they received diurnal cycles of light and dark (Table 2.1). Compared to germination at constant temperatures in the dark, daily alternation of temperature alone gave a significant increase in germination, but this was still much less than when light was available. There was no significant difference in germination at 20°C and 30°C. In the treatment of alternating temperature and light, the germination was significantly higher than in any other treatment.

Table 2.1: Mean germination* of freshly harvested yarrow seed after 28 days incubation at constant and alternating temperatures in the presence or absence of light.

Temperature (°C)	Germination (%)	
	Continuous Dark	8 h Light Day^{-1}
(a) Seed imbibed in distilled water		
20	4.0	85.3
30	3.2	82.8
20 - 30	42.3	92.0
# L.S.D. $_{0.05}$	3.1	
(b) Seed imbibed in 10^{-3}M KNO_3 solution		
20	43.3	83.3
30	43.2	83.7
20 - 30	81.7	96.0
# L.S.D. $_{0.05}$	3.1	

*Each value is a mean of 6 observations; germination counts were taken 28 days after incubation.

#L.S.D. value used for both vertical and horizontal comparison of means.

2.2.2.2 Effect of Moistening Agent and Light

In the presence of potassium nitrate solution there was a significant increase in the germination of yarrow seeds in the dark compared to when only water was present as the moistening medium (Table 2.2); but this was still significantly less than when light was available in the presence of water. High germination was obtained in the presence of light irrespective of the moistening medium.

Experiment 2: Effect of Low Temperature Stratification and Scarification on the Germination of Yarrow Seed

2.2.3 Materials and Methods

2.2.3.1 Seed Material

Mature, dehydrating seed heads were collected on 4 February 1981 from a naturally growing population of yarrow found close to the research fields at Lincoln College. These were dried in the sun for 4 days by spreading them out on a paper. Seed cleaning was performed as detailed in Section 2.2.1.1. The clean seed was immediately used in the experiment.

2.2.3.2 Experimental Design and Procedure

The experiment was designed to evaluate the effects of low temperature chilling (stratification), pricking (scarification) or the combination of both on the germination of freshly harvested yarrow seed. Each treatment was replicated 6 times and was completely randomized. The seeds were incubated at 25°C; the treatments were as follows:

1. in continuous dark;
2. pricked + continuous dark;
3. chilled for 1 week at 5°C + continuous dark;

Table 2.2: Mean germination* of freshly harvested yarrow seed imbibed in water or 10^{-3} M KNO_3 solution in the presence or absence of light.

Moistening Agent	Germination (%)	
	Continuous Dark	8 h Light Day^{-1}
(a) Incubation of seed at 20°C:		
Water	4.0	85.3
10^{-3} M KNO_3	43.3	83.3
#L.S.D. $_{0.05}$	2.5	
(b) Incubation of seed at 30°C:		
Water	3.2	82.8
10^{-3}M KNO_3	43.2	83.7
#L.S.D. $_{0.05}$	2.5	
(c) Incubation of seed at 20-30°C (alternating temperature):		
Water	42.3	92.0
16^{-3} M KNO_3	81.7	96.0
#L.S.D. $_{0.05}$	2.5	

*Each value is a mean of 6 observations; germination counts were taken 28 days after incubation.

Refer to Table 2.1.

4. pricked and chilled for 1 week at 5°C + continuous dark;
5. 8 h light day^{-1}.

On 8 February 1981, glass petri dishes were lined with Whatman grade 181 9 cm germination pads, and 100 yarrow seeds were placed in each dish to which 10 ml distilled water was added. The dishes destined to receive light were transferred into individual clear polythene bags, while all other dishes were immediately placed in individual black polythene bags. The pricking of seeds was done on the same day in a dark room under a green 'safe' light. Observations made earlier showed that this light had no effect on the germination of freshly harvested yarrow seed (Appendix 2). Individual seeds were pricked through the cotyledons using a fine pointed needle, taking care not to damage the embryo. After pricking the seeds, the dishes were replaced in the black polythene bags. The seeds to be chilled were placed in a refrigerator at 5°C while the seeds in the other treatments were incubated at 25°C in a growth chamber receiving 8 hours light day^{-1} of 3875 lux intensity from a similar source as detailed in section 2.2.1.3. On 15 February 1981, the chilled seeds were also transferred into the growth chamber. Germination counts were made after 28 days incubation at 25°C (i.e., on 15 March 1981 for the chilled seed and 8 March 1981 for all other treatments); all seedling plants and seeds with emerged radicles, 1 mm in length or more, were counted as germinated and removed from the petri dishes.

2.2.4 Results

Compared to the germination of yarrow seeds in continuous darkness, all other treatments gave significantly higher germination (Table 2.3). Pricking and chilling the seeds enabled approximately 48% of them to germinate and this was a significant increase when compared to the number of seeds germinating after chilling alone. There was no marked difference in ger-

mination between the seeds that were pricked or those that were pricked and chilled. Germination in the presence of light was significantly higher than in any other treatment (Table 2.3). The ability of approximately 10% of the seed to germinate in the absence of light at constant temperature suggests that some seed were only in a quiescent state. The ungerminated seed were tested for viability according to I.S.T.A. (1976) recommendations detailed in section 2.2; there was no loss in viability of the seed owing to the treatments.

Table 2.3: Mean germination of freshly harvested yarrow seed after 28 days of incubation at 25°C. Each value is a mean of 6 observations.

Treatment	Germination# (%)
1. 8 h light day^{-1}	97.0
2. Pricked + continuous dark	48.8
3. Pricked and chilled* at 5°C (1 week) + continuous dark	48.3
4. Chilled* at 5°C (1 week) + continuous dark	32.5
5. Continuous dark	9.8
C.V. (%)	6.5
L.S.D. 0.05	3.6

* Seeds were chilled in continuous darkness.

\# Seeds imbibed in distilled water.

Experiment 3: Establishment of Seedling Yarrow Plants from Surface-Sown Seed at Different Times of the Year

2.2.5 Materials and Methods

2.2.5.1 Experimental Procedure

Sun dried yarrow seed heads were collected in December 1978 from a natural population growing close to the research fields at Lincoln College. Seed cleaning was done as detailed in section 2.2; the seeds were stored in a black polythene bag at room temperature. Laboratory germination tests were carried out on samples drawn from this seed lot, 14 days before each monthly sowing, according to I.S.T.A. (1976) recommendations (refer section 2.2). A mean germination of 97% (S.E. 3%) was obtained throughout the experimental period (i.e., over one year).

Five hundred litres of Wakanui silt loam soil were collected from a research field near the College; it was sieved through a 2 mm mesh. At each monthly sowing of yarrow seed, a sufficient quantity of the sieved soil was steam sterilized in an autoclave for 1 h at a pressure of 1.1 kg cm^{-2} and 121°C, to kill all resident seeds. The soil was then filled into five plastic containers (16 x 16 x 18 cm each) which had drainage holes at the bottom. The soil was lightly compacted so that its surface was 3 cm from the top edge of the container.

On the first day of each month of 1979, 30 mg of yarrow seed (approximately 200 seeds) was sown onto the soil surface in each container and lightly covered (to < 1 mm depth) with a sprinkling of the same soil. The containers were then placed in the open environment in a polythene-lined trough and regularly irrigated from the bottom. The experiment was a completely randomized design.

Previous work (Kannangara, unpublished) showed that similarly sown yarrow seed, in the presence of light and adequate moisture, germinated fully in the summer and seedling establishment was completed by 21 days after sowing the seed. In the present experiment, where light was available to the seeds and adequate water was supplied, a seedling count was carried out 28 days after sowing. The seedlings were carefully removed from the containers after counting them. The containers were then transferred into a controlled environment chamber and supplied with adequate water, 8 h light day^{-1} (3875 lux intensity) from a similar source as detailed in section 2.2, and 20 - 30°C diurnal alternating temperature (higher temperature coincided with the time when light was available) for 21 days; a further seedling count was then carried out. Seedling establishment in the open environment was calculated as a percentage of the total number of seedlings emerging under both sets of conditions detailed above.

2.2.6 Results

In January, February, March, November and December, 98% to 99% seedling establishment occurred in the open environment (Fig. 2.1), while there was a significant decline in seedling establishment during the rest of the year. From April to June, seedling establishment decreased and there was no germination in July and August. From September onwards, seedling establishment increased significantly and reached a peak value in November.

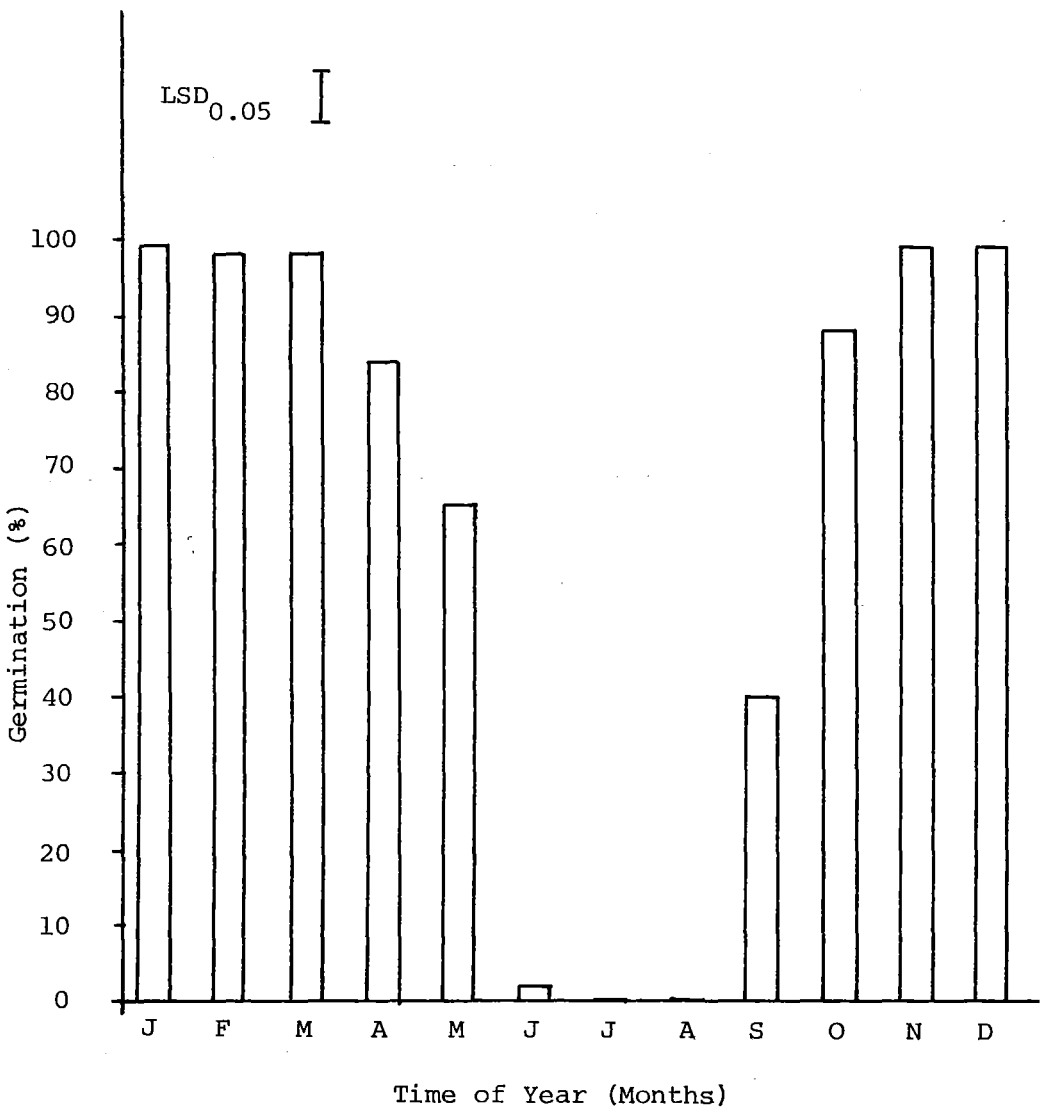

Figure 2.1: The establishment of seedling yarrow plants from surface-sown seed at different times of the year, in the presence of adequate moisture. Each value is a mean of five replicates.

Experiment 4: Effect of Depth and Duration of Burial on the Longevity of Viability of Yarrow Seeds

2.2.7 Materials and Methods

2.2.7.1 Experimental Procedure

Sun dried seed heads were collected on 27 March 1979 from a natural population of yarrow growing close to the research fields at Lincoln College. Seed cleaning and laboratory germination tests of the fresh seed were done as detailed in section 2.2; 98% (S.E. 2%) of the seeds germinated. Forty-two per cent of the seeds germinated in the dark at 20 - 30°C diurnal alternation of temperature; germination counts were made 28 days after incubation.

Templeton silt loam soil was collected from the seed burial site located at Henley, about 5 km from Lincoln College. The soil was sieved through a mesh and then steam sterilized as detailed in Section 2.2. Six hundred lots of 100 yarrow seeds each were counted; 10 g of sterilized soil was mixed with each seed lot and placed in separate fine mesh nylon cloth packets (4 x 4 cm) which were then sealed with 'Monel' stainless steel staples. The cloth mesh was fine enough to retain the seeds but still allow the free passage of water, gases, and micro-organisms.

On 28 March 1979, one hundred, 8.2 cm diameter holes were dug to a depth of 32 cm each, using a soil auger. The holes were placed at 50 cm intervals in two rows, 2 m apart. A nylon cloth packet, containing yarrow seed, was placed horizontally at the bottom of each hole (i.e., at 32 cm depth) and soil from the site was added and firmly compacted until the hole was 16 cm deep. In a similar way, other seed packets were buried at 16, 8, 4 and 2 cm in each hole. The packets on the soil surface (0 cm) were anchored in place by stainless steel drawing pins and the burial sites were clearly marked with coloured metal pegs. The ryegrass and white clover,

resident on the burial site, were allowed to grow over the burial sites but were clipped regularly to a height of approximately 4 cm.

2.2.7.2 Sampling Procedure

After 3, 6, 9, 12, 15, 18, 21, and 24 months of burial, seed packets were carefully exhumed from each depth and placed immediately in separate black polythene bags. The extraction of the packets was carried out from within a light-proof (black polythene lined) box using a green 'safe light' torch (refer Appendix 2). Eight sites were randomly selected at each time of sampling. In a dark room in the laboratory, the contents of each cloth packet were thinly spread on a Whatman grade 181 germination pad placed in a plastic tray (15 x 10 cm); green 'safe light' was used for this operation. To each tray, 25 ml of distilled water was added before transferring them to individual polythene pags: trays with seed from 4 burial sites were transferred into black polythene bags, while the others from the remaining sites were placed in clear polythene bags. The seeds were incubated in a controlled environment chamber with a 20 - 30^{o}C diurnal alternation of temperature. In addition to the temperature alternation, the seeds placed in clear polythene bags received 8 h light day^{-1} from a source as detailed in section 2.2; light availability coincided with the higher temperature period.

A germination count was made after a 28 day incubation period; all seedling plants and seeds with radicles of 1 mm or more in length were counted as germinated and removed from the trays. The contents of the trays were then lightly stirred and incubated for a further 21 days; all trays received the alternation of temperature and light treatment detailed above. No further germination occurred in the seeds that were formerly incubated in the light, while some of those that had been in the dark, germinated when they received light. Of the initial 100 seeds, the seeds that were unaccounted for were presumed to have perished in the soil.

2.2.8 Results

The figures 2.2 and 2.3 were drawn from the mean germination values given in Appendices 3 and 4, respectively.

After 3 months exposure to the ambient conditions in the field, 3% or less of the yarrow seed, at 0 cm, 16 cm, and 32 cm depths in the soil, were able to germinate in the dark, even in the presence of alternating temperature (Fig. 2.2). Compared to the seeds at the above depths in the soil, significantly[#] higher numbers at 2 cm, 4 cm and 8 cm germinated in the dark up to 6 months after burial. However, from 9 months after burial, there was no significant difference in the dark germination of yarrow seed at all depths, and in all cases it was low. When the seed was subsequently transferred to light, the germination was similar to that represented in Fig. 2.3.

The germination of seed when supplied with the ideal ambient conditions could be a direct indicator of their viability. Thus, the ability of the yarrow seed to germinate in the presence of light and alternation of temperature (refer I.S.T.A., 1976 recommendations for germination of yarrow seed) after an increasing length of time of burial at different soil depths, indicates the longevity of viability of these seeds. In the present experiment, as the depth of burial increased, the yarrow seeds remained viable for longer periods of time (Fig. 2.3); the most rapid loss of viability occurred at the soil surface. Less than 8% of the seeds at the soil surface and at 2 cm depth in the soil remained viable after 12 and 15 months exposure to the ambient conditions in the field, respectively.

At 16 cm and 32 cm depths in the soil, more than 94% of the yarrow seed remained viable for up to 12 months after burial and even after a further 12 months had passed 51% and 67% of the original amount of seed retained viability at 16 cm and 32 cm depths, respectively. The seed buried at 4 cm and 8 cm showed intermediate effects to those detailed above.

[#] Refer to Appendix 3 for $L.S.D._{0.05}$ values.

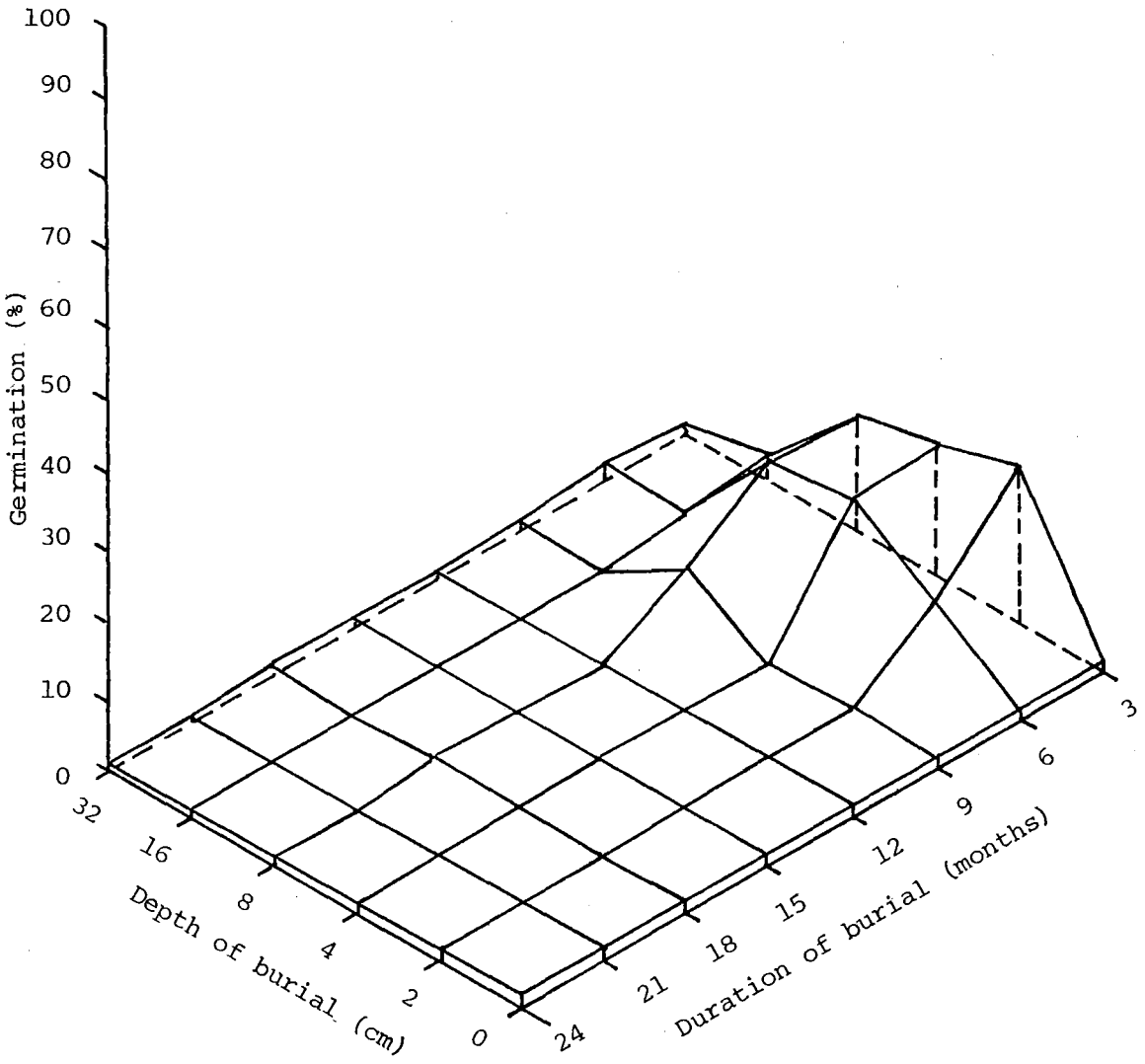

Figure 2.2: Effect of depth and duration of burial on the ability of yarrow seed to germinate in the dark in diurnal alternating temperatures of 20 - 30°C. Germination counts were made 28 days after incubation.

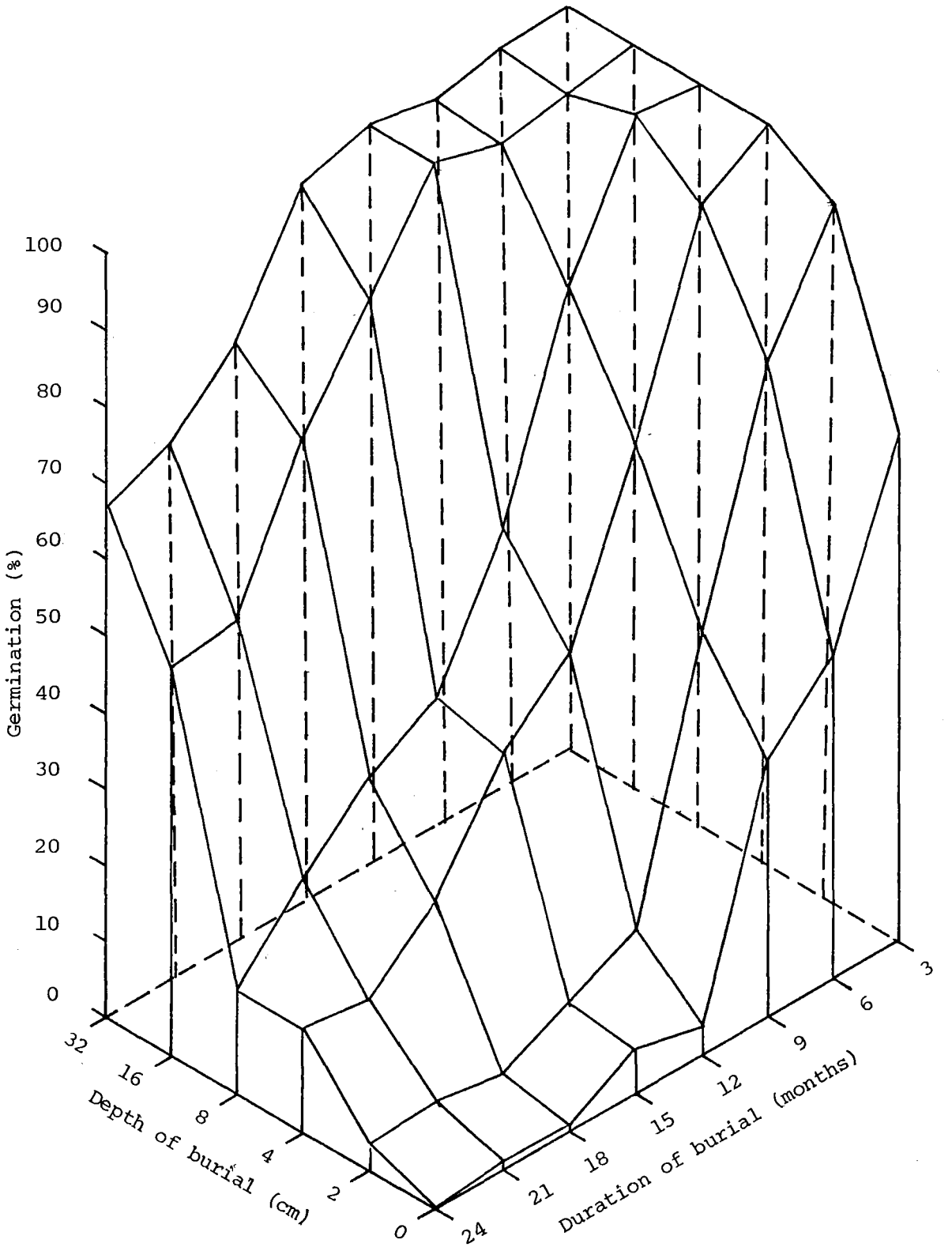

Figure 2.3: Effect of depth and duration of burial on the longevity of viability of yarrow seed. Germination tests were carried out according to I.S.T.A. (1976) recommendations; it is assumed that the seeds that failed to germinate after incubation for 28 days had lost viability.

2.3 DISCUSSION

Apart from the basic requirements of a temperature level which is not excessively high or low, adequate moisture and proper aeration, the seeds produced by certain species of plants need additional specific environmental cues for them to undergo normal germination (I.S.T.A., 1976). The seeds produced with such special needs for germination are dormant. Over 90% of the fresh seed produced by yarrow plants had a requirement for light (Tables 2.1, 2.2, 2.3), to germinate. However, alternation of temperature (Table 2.1) or the availability of nitrate ions (Table 2.2) was able to substitute for the light requirement of approximately 40% of these seeds. Therefore, a greater proportion of the yarrow seed produced are innately dormant. These results are consistent with the findings of Robocker (1977) and Bostock (1978). The germination of freshly harvested yarrow seed, in the absence of light, was enhanced by scarification and stratification (Table 2.3). Previously, Bostock (1978) had found that stratification increased the number of yarrow seeds requiring light for germination. Though the results from the present study appear to contradict Bostock's findings, the dry storage of yarrow seed at $3^{o}C$ for 3 months before they were used in his experiment may have changed the dormancy characteristics of a proportion of them, leading to the increase in the number of seeds requiring light for germination.

The thin coat of the yarrow seed and its quick response to environmental cues (the first signs of radicle emergence in these seeds was observed within 3 days after imbibition) indicates that dormancy is associated with physiologically immature embryos and/or the presence of germination inhibitors. Morphological immaturity of the embryos could not be responsible for dormancy of yarrow seed. If this was the case, the fresh seed would need a longer period for after-ripening and subsequent germination in response to the environmental cues (Stokes, 1965). The details of

the mechanisms by which the presence of light, alternation of temperature, availability of nitrate ions, and stratification and scarification, break the dormancy of the yarrow seeds are not known. However, it has been suggested by many workers that they are responsible for changing the level of germination inhibitors and promoters in the seeds (e.g., Mayer and Poljakoff-Mayber, 1975; Villiers, 1975; Lewak and Rudnicki, 1977; Thomas, 1977); in promoting the rehydration, synthesis, and maintenance of high levels of the form of phytochrome effective in inducing germination (i.e., P_{fr}) (e.g., Toole, 1973); and in promoting the oxidation of inhibitors in the seed (e.g., Wareing and Foda, 1957; Porter and Wareing, 1974). Depending on the mechanism(s) of dormancy in yarrow seed, one or more of these effects may be involved in inducing the seeds to germinate in the presence of specific environmental cues.

Bostock (1978) reported the presence of at least 3 types of conditionally dormant yarrow seeds. In the present study, it was possible to indentify yarrow seed which had an absolute requirement of light and those that can germinate when temperature alternations and/or nitrate ions were present (Tables 2.1, 2.2). The germination of some seeds was also promoted by stratification or scarification (Table 2.3). The production of these types of conditionally dormant seeds by yarrow plants may be of strategic importance to its survival in the constantly disturbed soil of arable lands. When these seeds are buried at shallow depths in the soil and do not receive light, the non-dormant yarrow seeds (Table 2.3) can germinate and make an effort to establish seedling plants. Even if these plants fail to survive, other yarrow seeds are present in the soil which can undergo staggered germination when their specific needs of alternation of temperature, availability of sufficiently high concentrations of soil nitrate, stratification, or scarification is satisfied. This increases the chance of at least a few seedlings establishing successfully. In addition, the presence of yarrow seed with the absolute requirement of a

light stimulus for germination ensures that even if all other types of conditionally dormant seeds are exhausted, still more seed reserves remain in the soil and can continue to produce seedling plants once these are brought up to the soil surface by cultivation or other agencies. The light availability, alternations of temperature, and concentrations of nitrates at the soil surface and the upper layers of the soil are comparatively higher in open situations than in habitats covered with vegetation (Thompson, Grime and Mason, 1977; Hart, 1978). The ability of yarrow seeds to respond positively to these ambient conditions ensures that their germination mainly occurs when the seeds are on or close to the soil surface and when possible interference from other plants, that may be already established, is sparse or is totally absent. Thus, the characteristics of conditional dormancy in yarrow seed enables the species to overcome the possibility of a speedy exhaustion of its seed reserves from the soil seed-bank and increases it chances of successfully establishing seedling plants.

In the Canterbury Plains of New Zealand, where cropping is carried out either under purely rainfed conditions or with supplementary irrigation, the soil may be cultivated from spring through to autumn. The high germination of yarrow seed lying on the soil surface and their successful establishment throughout this period in the presence of adequate moisture (Fig. 2.1) may be of prime importance in contributing to yarrow being a problem weed in many crops (e.g., beans, field peas, beet, and white clover).

Taylorson (1970), stated that when weed seeds are present in the soil, a number of factors, including differences in exposure to light, moisture, temperature, and gaseous environments, often simultaneously interact with them. Depending on the depth of placement of the seeds in the soil profile and the season of the year, the quantitative and qualitative exposure of the seeds to these factors can differ considerably. This in turn may affect the dormancy characteristics and the longevity of viability of

the seed. After 3 months of burial in the soil at 16 cm and 32 cm, the initial ability of 42% of the yarrow seed to germinate in the dark in alternating temperature (refer section 2.2.7.1) was more markedly decreased than in the seeds buried at 2 cm, 4 cm, and 8 cm depths (Fig. 2.2; Appendix 3). However, the viability of these seeds at the time of burial and 3 months later did not differ a great deal when germination was carried out in the presence of light and alternation of temperature (Fig. 2.3; Appendix 4). From 9 months onwards, the yarrow seed at all depths in the soil had almost completely lost their ability to positively respond to alternation of temperature in the dark (Fig. 2.2) and needed a light stimulus to germinate (Fig. 2.3). These results indicate that with increasing depth of burial there was a more rapid loss of yarrow seed that can subsequently respond positively to alternations of temperature in the dark. Even the quiescent seeds of yarrow were induced into a dormancy condition where they required a light stimulus to germinate. Stokes (1965) stated that if certain dormant seeds, which are capable of germinating when requirements for special environmental cues are satisfied, are prevented from germinating owing to the presence of some inhibitory or suboptimal ambient condition(s), they acquire different dormancy characteristics. This appears to occur to a proportion of the yarrow seed that is buried in the soil.

Yarrow lying on the soil surface or at shallow depths in the soil lost their viability at a markedly faster rate than those buried deeper in the soil profile (Fig. 2.3). These results are in agreement with findings on the longevity of seed viability in other plant species (e.g., Toole, 1946; Rampton and Ching, 1966; Dawson and Bruns, 1975). The lower variability of temperature from season to season (Appendix 1), the increasingly low oxygen and high carbon dioxide concentrations (Bibbey, 1948), and the decreasing activity of pathogens and insects (Taylorson, 1970) in the deeper layers of the soil profile may be responsible for the greater

longevity of variability of the yarrow seeds. More work is needed to identify the exact ambient factor(s) that increase the longevity of viability of the seeds buried deeper in the soil. This could enable the possible modification of these factors by various means such as the deeper cultivation of the soil for better aeration and greater temperature fluctuations. This may lead to a consequential reduction in the longevity of viability of the yarrow seeds present in the soil seed-bank. Apart from these findings, other work has shown that yarrow seeds on the soil surface lost their viability after a wheat stubble burn (Kannangara, unpublished); seeds at a depth of 1 cm or more were unaffected. Therefore, stubble burning immediately after crop harvesting can destroy large quantities of seed which may otherwise be incorporated into the soil by subsequent tillage operations. This can be very effective in reducing the yarrow populations in the coming years.

CHAPTER 3

EFFECT OF DIFFERENT LIGHT INTENSITIES ON SURVIVAL, DRY MATTER ACCUMULATION, AND REPRODUCTIVE EFFORT OF SEEDLING YARROW

3.1 INTRODUCTION

In natural situations, angiospermous plant species grow in open sites, moderately shaded habitats or under canopy covers where only a low level of light is available. Plant species adapted to grow in shaded habitats (shade tolerant species) have lower rates of photosynthesis and respiration and low relative growth rate (RGR) compared to species adapted to grow in open situations (shade-intolerant species) (Grime, 1965). These characteristics of shade tolerant species enable them to exhibit a greater carbohydrate economy than the shade intolerant species when growing in habitats of reduced light availability.

Mortality of seedlings in shaded habitats is mainly due to fungal attack (Grime, 1965). He has suggested that, owing to the carbohydrate economy of the shade tolerant species, their tissues may have comparatively higher levels of sugar than in shade-intolerant species thereby enabling them to resist fungal infection. For example, the seedlings of shade tolerant species like *Gleditzia triacanthos* and *Quercus rubra* had fewer fatalities compared to the seedlings of *Betula populifolia, B. lenta,* and *Rhus glabra*, which are shade-intolerant species, when grown in deep shade (Grime, 1965). Apart from enabling greater resistance to fungal attack, the high levels of sugar, if maintained by the shade tolerant species when the incident light is reduced by overhead canopies, will also enable their continued growth under shaded conditions (Packham and Willis, 1977).

Grime (1965) found that many shade-tolerant genera (e.g., *Pachysandra* spp. and *Hedera* spp.), whether they were grown in direct sunlight or in shade, had thick leaves and leaf arrangements which result in considerable self-shading. From these observations he suggested that carbohydrate solvency of these plants may primarily depend on conservation of the light energy received by them rather than the efficiency of its capture.

Within pastures and crop stands, small differences in height generally lead to large changes in the intensity, direction, and quality of light available. Therefore, the success of a plant species growing in association with pasture plants or crops may depend on their ability to avoid shade; this in turn depends upon the height, aspect and/or inclination of their leaves. Grime and Jeffrey (1965) found that a species like *Castanea mollissima*, which has large seed reserves (source of energy) and a series of extension sites, was capable of rapid extension on shading and suffficient mechanical tissue was available to maintain the shoot in an erect position. However, in other species, where seed reserves are low and there is a limited availability of sites for rapid vertical growth, their ability to survive in shaded habitats may be dependent on their efficient cabohydrate economies (Grime, 1965) and/or availability of certain other special mechanisms (e.g., substances with fungicidal effects) which prevent or decrease their mortality.

Many workers have reported the decline in net assimilation rates (NAR) and increase in leaf area ratios (LAR) as the light availability to plant species declined (e.g., Blackman and Wilson, 1951a, b; Hughes and Evans, 1962; Pandey and Sinha, 1977; Patterson, 1982). Blackman and Wilson (1951b) found that in the plant species they studied, which included species which naturally grew in shaded habitats (e.g., *Geum urbanum* and *Solanum dulcamara*) and open situations (e.g., *Pisum sativum* and *Fagopyrum esculentum*), the rate of increase in LAR in the 'shade habitat' species was

generally much greater than in the others when the plants were shaded. However, the NAR and light compensation point values of all these species were not very different from each other. They re-defined shade-tolerant species as those in which there is a rapid increase in LAR, from an initially low value, when they are shaded. The converse was said to characterise shade-intolerant species. In shade-tolerant species, the rapid increase in LAR, with shading, compensates for the decline in NAR and thus maintains their RGR[#] at a sufficiently high level to ensure good growth (Hughes, 1966; Pandey and Sinha, 1977); the converse is true for shade-intolerant species.

The changes that occur to the total dry weight of a plant species, when subjected to shade, is the net result of the variations in the growth and development of its roots, vegetative reproduction organs, stems, leaves, and the sexual reproductive system.

Compared to plants growing in an open environment, the root dry weights of seedling *Achillea millefolium* receiving 46.8%, 23.7% and 6.4% of full daylight were 22%, 53%, and 91% less, respectively, after 28 days growth (derived from Bourdôt, 1980, p. 245). The root weight ratios (RWR), calculated from Bourdôt's results, show that the proportion of the total biomass of the plant allocated to the roots declined with increasing shade. Similar findings of the reduction in root weight with shade have been seen in many species, including *Bromus inermis* (Watkins, 1940); *Lolium perenne, Dactylis glomerata, Paspalum dilatatum, Trifolium repens, T. subterranean* and *Lotus uliginosum* (Mitchell, 1954); and *sorghum halepense* (McWhorter and Jordan, 1976). Even in *Impatiens parviflora,* a well-known shade-tolerant species, similar trends were evident when the light availability to the plant declined (Hughes, 1965).

The number of rhizomes plant^{-1}, the total rhizome length, and the number of rhizome nodes plant^{-1} in *Sorghum halepense* declined as the light availability to the plant decreased (McWhorter and Jordan, 1976). The

[#]Relative growth rate.

length and diameter of the rhizomes in *Imperata cylindrica* decreased with shade, but their internode length and bud number node^{-1} remained unaffected Eussen, 1978). In both these species, the net effect of these morphological changes was a reduction in the dry weight of the rhizomes. In many other species, including *Cynodon dactylon* (Burton, Jackson and Knox, 1959) and *Agropyron repens* (Williams, 1970), similar decreases in rhizome weight occurred with shading of the plants. The rhizome weight ratios (R_zWR) of *Imperata cylindrica* (Patterson, 1980), *Cyperus rotandus* and *C. esculentus* (Patterson, 1982), and *Agropyron repens* (derived from Williams, 1970) decreased with shading, indicating the decline in their vegetative reproductive effort. In *Achillea millefolium* plants, grown in pots in full daylight, 26% of the total dry matter was allocated for vegetative reproduction (Bostock and Benton, 1979). There is no information on the effect of shade on vegetative reproduction of this species.

The respective stem and flowering stem dry weights of *Imperata cylindrica* (Patterson, 1980) and *Achillea millefolium* (Bourdôt, 1980) and their leaf dry weights declined with increasingly higher levels of shading of the plants. They also found that the proportion of the total biomass partitioned to the stem fraction decreased, while a higher proportion of dry matter was partitioned to leaves of these plants, with increasing shade. Similar findings were reported in *Cyperus rotandus* and *C. esculentus* (Patterson, 1982). The higher biomass allocation to the leaves may be an effort by the plant to provide a leaf area which is able to intercept sufficient light from an already depleted source. However, in *Impatiens parviflora*, which is adapted to grow in a range of light levels, the stem and leaf weights increased and a higher proportion of total biomass was allocated to them as the plants were shaded (Hughes, 1965).

Many workers have shown that developmental and growth changes occur in the sexual reproduction system of plant species depending on the light availability in the habitats in which they grow. For example, in

Cyperus rotandus (Sendoya and de Dok, 1975) and *C. esculentus* (Keeley and Thullen, 1978) flowering became less abundant, and was completely absent at low light intensities, while flower formation, blossoming of flowers, and seed ripening in *Portulaca oleracea* was delayed by shade (Noguchi and Nakayama, 1978a). Seedling plants of *Achillea millefolium* were observed to initiate flowering stems in full daylight and at 46.8%, 23.7% and 6.4% full daylight (Bourdôt, 1980). However, he grew the plants for 5 weeks in controlled environmental conditions, where they received artificial light equivalent to approximately 20% summer daylight for 16 hours day^{-1}, prior to transferring them to the above-mentioned light levels. This pretreatment may have satisfied the light requirements of the plants for flowering, and thus his observations in this respect are in doubt. Bostock and Benton (1979) found that in pot-grown *Achillea millefolium* plants which flowered, 21.5% of total dry matter was allocated for seed reproduction (i.e. to the peduncles, capitula, perianth, pericarps, and embryos). There is no published literature on the effect of shade on sexual reproduction of yarrow.

The present study was undertaken to evaluate the ability of seedling yarrow plants to survive in habitats of reduced light availability and the effect of shade on biomass production and the reproductive effort of the yarrow plants. In nature, there is often a high correlation between changes in one aspect of the environment and changes in another, and these correlations cannot always be broken down by field studies alone. In field studies using artificial shades, the dynamic variations in light availability as the plants grow, its spatial distribution, the occurrence of sunflecks, important differences in the spectral composition of light filtered through the upper canopy, etc. are not taken into account. Even though the above drawbacks are present in a semi-natural study of this kind, it helps to gather important preliminary information regarding the trends of plants in response to varying light intensities. Evans and Hughes (1961)

pointed out the importance of combining the results of observations under natural and semi-natural conditions to obtain a better understanding of the relationships between the plants and the aerial environment. Hence, this study was carried out to obtain a preliminary insight into the behaviour of seedling yarrow plants when growing at different constant light intensities.

3.2 MATERIALS AND METHODS

3.2.1 Experimental Procedure

3.2.1.1 Design of Experiment

Seedling plants of yarrow (*Achillea millefolium*) were grown at 4 different light intensities; in full sunlight and 3 shade levels. The adjacent plots were spaced 3 m apart to prevent mutual shading. Each treatment was replicated 6 times and the experiment was arranged as a randomized complete block.

3.2.1.2 Establishment and Management

Sun dried yarrow inflorescences were collected in April 1979, from plants growing close to the research fields at Lincoln College, and stored in polythene bags at room temperature until November 1979 when the extracted seeds were used in the experiment. Seed extraction was carried out as detailed in Chapter 2.

Two hundred and fifty, 10 cm long, polythene tubes of 2 cm internal diameter were filled with Wakanui silt loam soil from the experimental site and placed in a wooden seed flat. On 1 November 1979, 2 yarrow seeds were placed in each tube and lightly covered with soil. The tubes were frequently bottom watered after placement in the field close to the experimental site. Seeds germinated in 3 to 4 days and were thinned to 1 seedling $tube^{-1}$, 1 week later.

The planting sites in the plots were marked out at a spacing of 30 cm between adjacent plants; each plot having 3 rows of plants with 4 planting sites in each row. 'Planter bags' made of black horticultural grade polythene (30 x 30 x 50 cm) and having 10 drainage holes at the bottom of each, were buried at the two inner planting sites of the middle row of each plot after filling them with shredded Wakanui silt loam soil. The upper ends of the bags were flush with the soil surface. These bags were used so that roots and rhizomes (if any) could be sampled without damage. Only the plants grown in these bags were sampled.

On 17 and 18 November 1979, two-week old healthy yarrow seedlings of similar size, which had developed the first pair of true leaves, were removed from the tubes and planted in the field plots at the rate of one seedling per planting site. The selection of seedlings of similar size was done to ensure that the biological material used in the experiment was phenotypically uniform at the outset of the experiment. Water was supplied to each planting site via a trickle irrigation line, and soil was maintained at field capacity throughout the experiment.

Frames of the rectangular shade houses, each measuring 1.8 x 1.6 x 1.0 m, were made from 13 mm steel rods. Black 'Sarlon' polyshade cloth of three different densities (recommended by the manufacturer, Sarlon Reid Ltd, Auckland, to transmit known amounts of light) was draped on the frames so that 3 sets of 6 shade houses each were constructed; each set having a different level of light transmission. The cloth was firmly stretched on the frame and stitched onto it. A flap of cloth was left unstitched so as to enable entry into the shade house once it was erected over the plot. Bourdôt (1980) reported that the spectral quality of the light transmitted through these shade fabrics did not change in comparison to direct sunlight.

One week after transplanting the seedlings in the field (24 - 25 November 1979), the shade houses were erected on the appropriate

plots, ensuring that the side with the unstitched flap of cloth was facing the south. The orientation of the shade houses in this manner was to prevent the transmission of direct light on to the plants during times of entry. The flap of cloth was temporarily fastened on to the frame of the shade house using wire clips. All boarder plants in each plot were more than 40 cm inside the sides of the shade house, ensuring that direct light from the gap between the soil level and bottom edge of the shade cloth did not reach the plants at any time of the day. This 10 cm gap between soil level and shade house allowed free movement of air; it also allowed insects (e.g., Dipterans) access to the yarrow inflorescences, thus ensuring cross pollination. The mesh-like nature of the shade cloth allowed the movement of air through the shade houses, though a certain degree of sheltering from the wind was evident.

On 24 November 1979 (clear day, totally free of clouds), between 1300 and 1400 hours (N.Z.S.T.), the total photosynthetically active radiation (PAR) transmitted to ground level, both inside and outside the shade houses, was measured using a Li-cor C-275 quantum sensor. The PAR inside the shade houses was 46.8%, 23.7% and 6.4% of the outside value. The ambient air temperature in the open and within the different shade houses of one replicate was recorded from 7 to 13 February 1980 (Appendix 5) using a maximum/minimum mercury thermometer.

3.2.2 Observations

The time taken from seed germination to the appearance of the first visible signs of flowering (i.e., the appearance of clusters of capitula at the centre of the rosette plant) was determined for plants grown at the different light intensities, by weekly observation. All plants at a particular light intensity flowered at the same time.

3.2.3 Sampling Procedure

The first sampling was carried out on 14 April 1980 when inflorescences of plants grown at full daylight were dehydrating; a single plant being removed from each plot. The clusters of capitula on the remaining plant at 46.8% and 23.7% daylight were tagged, using fine gauge, plastic coated wire to distinguish them from new capitula formed later.

After washing the soil from the subterranean portions of the sampled plant it was fractionated into roots, primary and secondary rhizomes, aerial stems, leaves, and capitula. Since the flowering stems bear cauline leaves and capitula it has both vegetative and reproductive functions. Thus the capitula were considered as the sexual reproductive fraction; the cauline leaves and the stem of the flowering unit were included in the leaf and aerial stem fraction respectively.

Counts were made on the numbers of primary and secondary rhizomes plant^{-1}, rhizome buds plant^{-1}, flowering stems and capitula plant^{-1}. The total length of primary and secondary rhizomes were measured separately. A sub-sample of 100 capitula was randomly selected from the total number of capitula on each plant grown at full daylight; each capitulum was dissected and the number of seeds counted to determine the mean number of seeds capitulum^{-1}. The product of the mean number of seeds capitulum^{-1} and number of capitula plant^{-1} gave an estimate of seed production plant^{-1}.

After collection of the above detailed data, the different plant fractions were dried at 80^{o}C to constant weight.

The second sampling was carried out on 14 June 1980 when inflorescences on the plant at 46.8% and 23.7% daylight were dying back. Dieback was due to the low temperature prevailing at this time (Appendix 1); seed heads were not fully mature. The capitula formed after the first sampling did not mature any seed and were discarded; only the tagged clusters of capitula were used. The seed capitulum^{-1} was determined as

detailed above. Estimations of seed production plant^{-1} at 46.8% and 23.7% daylight were made using the respective values of capitula plant^{-1} from the first sample and values of mean seeds capitulum^{-1} from the second sample.

3.2.4 Statistical Procedure

An analysis of variance was carried out on each of the following sets of data:

(i) The dry weights of: roots; primary rhizomes; secondary rhizomes; leaf; stem; capitula; and total dry weight.

(ii) Number of: flower stems; capitula; seeds plant^{-1}; seeds capitulum^{-1}.

(iii) Number of: primary rhizomes; secondary rhizomes; rhizome buds plant^{-1}.

(iv) Length of: primary rhizomes; secondary rhizomes.

(v) Seed:rhizome bud number.

(vi) The weight ratios of: roots; rhizomes; stems; leaf; capitula.

(vii) Capitula:rhizome weight ratio.

3.3 RESULTS

3.3.1 Plant Survival

There was no mortality of yarrow plants with increasing shade; the plants at 6.4% daylight were much smaller than the plants at other light intensities.

3.3.2 Sexual Reproduction

3.3.2.1 Flowering Time and Flower Stems

The time taken for the appearance of clusters of capitula at the centre of the rosette of leaves was delayed by increasing levels of

shade; the respective times for plants at 100%, 46.8% and 23.7% daylight being 13, 15 and 16 weeks after seedling emergence. There was no flowering at 6.4% daylight after 23 weeks of growth, the plants remaining as rosettes.

The number of flowering stems formed declined with increasing levels of shade (Table 3.1); there were significantly fewer flowering stems at 23.7% daylight compared to plants growing at 46.8% daylight and full daylight.

3.3.2.2 Capitula Plant^{-1} and Seed Capitulum^{-1}

The capitula plant^{-1} and seed capitulum^{-1} declined significantly with increasing shade (Table 3.1). There was approximately a 4% and 42% decrease in the number of capitula per flowering stem at 46.8% and 23.7% daylight respectively, compared to plant grown in full daylight. This indicated that the decline in the number of capitula plant^{-1} was due to the reduction in the flowering stems plant^{-1} and the decline in the number of capitula produced on each flowering stem present.

3.3.2.3 Seeds Plant^{-1}

There was a decline in the number of seeds produced as the light available to the yarrow plant decreased (Table 3.1). This was the net result of the decrease in numbers of flowering stems plant^{-1}, capitula plant^{-1}, and seeds capitulum^{-1}.

3.3.3 Vegetative Reproduction

3.3.3.1 Rhizome Number and Length

The number and length of the primary rhizomes, and the secondary rhizomes declined with decreasing availability of light to the seedling yarrow plants (Table 3.2). Compared to plants growing in full daylight, the primary and secondary rhizome numbers and their lengths at 46.8%

Tabel 3.1: Effect of different light intensities on sexual reproduction in seedling yarrow.

Plant Component	Mean Number					
	Light Intensity* (%)					
	100	46.8	23.7	6.4	$LSD_{0.05}$	C.V. (%)
Flowering stems plant^{-1}	4.8	2.8	1.2	0	1.5	38.6
Capitula plant^{-1}	1039.0	582.0	150.0	-	340.6	44.9
Seeds capitulum^{-1}	20.2	8.5	2.0	-	3.0	22.4
Seeds plant^{-1}	20552	5152	296	-	5105.7	45.8

*Percentage photosynthetically active radiation (PAR); 100 = full daylight.

Table 3.2: Effect of different light intensities on vegetative reproduction of seedling yarrow. Each value is a mean of 6 plants.

Plant Components	Mean Number and Length					
	Light Intensity* (%)					
	100	46.8	23.7	6.4	$LSD_{0.05}$	C.V. (%)
Primary rhizome plants^{-1}	58.8	42.8	28.7	4.5	4.9	10.1
Secondary rhizomes plant^{-1}	35.3	3.7	2.3	0	4.7	16.5
Length of primary rhizomes (cm)	818.3	543.5	445.8	62.7	50.0	7.4
Length of secondary rhizomes (cm)	432.3	29.0	22.7	-	22.0	12.6
Rhizome buds plant^{-1}	841.2	258.8	242.5	33.2	18.8	8.8

*Percentage photosynthetically active radiation (PAR); 100 = full daylight.

23.7% and 6.4% daylight were significantly less. At 6.4% daylight, the number and total length of primary rhizomes were significantly less than their corresponding values at 100%, 46.8% and 23.7% daylight; no secondary rhizomes were present at the lowest light intensity.

3.3.3.2 Rhizome Buds

The rhizome buds plant^{-1} declined with increasing shade; a significantly lower number being present at 46.8%, 23.7% and 6.4% daylight than at full daylight (Table 3.2). Seedling yarrow growing at 6.4% daylight had 4%, 13% and 14% of the number of rhizome buds present at 100%, 46.8% and 23.7% daylight, respectively.

3.3.4 Seed:Rhizome Bud Number Ratio

The Yarrow plant growing in full daylight had approximately 25 seeds for every rhizome bud that was present, and there was no significant change in the ratio at 46.8% daylight (Table 3.3) even though the seed and rhizome bud numbers declined with decreasing availability of light to the plant (Tables 3.1, 3.2). At 23.7% daylight, seed production declined more rapidly than rhizome bud production, leading to a significant decrease in the ratio (Table 3.3); there was approximately 1 seed for every rhizome bud present.

3.3.5 Dry Weight

As the light available to the seedling yarrow plant declined, the weights of the root, rhizome, leaf, stem and capitula fractions decreased, leading to the reduction in the total dry weight of the plant (Table 3.4). The weights of all plant fractions at 46.8%, 23.7% and 6.4% daylight were significantly less than their corresponding values at full daylight. The weights of the root, rhizome, leaf and stem fractions at 6.4% daylight were

Table 3.3: The ratio of seed and rhizome bud number in seedling yarrow grown under different light intensities.

Light Intensity* (%)	Mean Ratios
	Seed:Rhizome Bud Number
100	24.5
46.8	19.9
23.7	1.2
6.4	-
$LSD_{0.05}$	10.2
C.V. (%)	52.1

*Percentage photosynthetically active radiation (PAR); 100 = full daylight.

Table 3.4: Effect of different light intensities on the dry weight of plant components of seedling yarrow. Each value is a mean of 6 plants.

Plant Components	Mean Values Plant^{-1} (g)					
	Light Intensity* (%)					
	100	46.8	23.7	6.4	$LSD_{0.05}$	C.V. (%)
Root	8.4	4.4	3.7	0.4	0.6	5.8
Primary rhizome	12.7	5.6	5.6	0.4	3.1	3.3
Secondary rhizome	3.1	0.4	0.2	-	0.2	25.8
Leaf (inclusive of dead leaves)	21.8	17.3	12.9	2.2	3.0	12.2
Stem	14.7	11.1	7.1	0.3	4.0	33.0
Capitula (with seed)	9.7	4.4	2.4	-	0.2	5.9
Total	70.4	43.2	31.9	3.3	10.2	22.0

*Percentage photosynthetically active radiation (PAR); 100 = full daylight.

approximately 5%, 3%, 10% and 2% of their corresponding values at full daylight. The total dry weight of the yarrow plant at each light level was significantly different from the others (Table 3.4).

3.3.6 Biomass Allocation

3.3.6.1 Partitioning of Dry Matter to Non-Reproductive Components

As indicated by their respective root weight ratios (RWR), there was no marked change in the proportion of the total biomass allocated to the roots of the yarrow plants at 100%, 46.8% and 23.7% daylight (Table 3.5). A significantly lesser proportion of total dry matter was allocated to the roots of the plant at 6.4% daylight. The amount of the total available dry matter allocated to the stems (i.e., SWR) declined with increasing shade; a significantly lower proportion being in the stems at 6.4% daylight compared to the plants growing in full daylight. However, the leaf weight ratios (LWR) of yarrow increased with decreasing shade and was significantly higher at 6.4% daylight, compared to plants growing at other light intensities. This shows that an increasing proportion of the total biomass was allocated to the leaves as the plant was shaded.

3.3.6.2 Partitioning of Dry Matter to the Rhizomes and Capitula

At full daylight, approximately 21% and 14% of the total biomass was partitioned to the rhizomes and capitual fractions of seedling yarrow plants, respectively (Table 3.5). As the light availability declined, the proportion of the total biomass allocated to the rhizomes (i.e. $R_z WR$) and capitula (i.e., CWR) declined; significantly lower proportions of the total available dry matter were in the rhizome and capitula fractions of the plants at 6.4% and 23.7% daylight, respectively. There was no flowering of the yarrow plant at 6.4% daylight (Section 3.3).

Table 3.5: Effect of different light intensitives on the root weight ratio (RWR), rhizome weight ratio (R_zWR), stem weight ratio (SWR), leaf weight ratio (LWR) and capitula weight ratio (CWR) of seedling yarrow.

Light Intensity* (%)	RWR	R_zWR	SWR	LWR	CWR
100	0.17	0.21	0.27	0.21	0.14
46.8	0.18	0.15	0.26	0.31	0.10
23.7	0.17	0.13	0.23	0.41	0.06
6.4	0.12	0.12	0.09	0.67	-
$L.S.D._{0.05}$	0.03	0.08	0.17	0.20	0.07
C.V. (%)	11.3	22.1	19.7	31.7	22.0

*Percentage photosynthetically active radiation (PAR); 100 = full daylight.

In the yarrow plant growing in full daylight, for every unit of dry matter present in the rhizomes, there was 0.61 of a unit of dry matter in the capitula (Table 3.6). The ratio of capitula to rhizome weight was significantly decreased at 23.7% daylight compared to higher light intensities, indicating that capitula growth was more affected than rhizome growth.

Table 3.6: The ratio of the weights of capitula to rhizomes in seedling yarrow under different light intensities.

Light Intensity* (%)	Mean Capitula:Rhizome Weight Ratio
100	0.61
46.8	0.73
23.7	0.41
6.4	-
$LSD_{0.05}$	0.16
C.V. (%)	21.5

*Percentage photosynthetically active radiation (PAR); 100 = full daylight.

3.4 DISCUSSION

Seedling yarrow plants survived in habitats receiving full daylight to 6.4% of full daylight, there being no plant mortality (Section 3.3.1). These findings are in agreement with similar studies carried out by Fenner

(1978) and Bourdôt (1980). From the above studies, it is not possible to isolate the possible mechanism(s) involved that enable this plant to adapt to such a wide range of light levels and to avoid mortality. However, as suggested by Grime (1965) for other shade-tolerant plant species, yarrow seedlings may be able to adjust their respiration rate in response to the decreasing photosynthesis that occurs at declining light levels and thereby conserve the available carbohydrates. This would enable it to maintain high levels of sugars in its tissues and thus resist fungal attack, and also continue growth (Packham and Willis, 1977), though at a much slower rate than in the plants growing in full daylight (Fenner, 1978). It is also possible that the aromatic substances present in the yarrow seedlings (Chandler, Hooper and Harvey, 1982) may have a fungicidal effect, thus preventing the mortality of these seedlings in shaded environments. Further work needs to be carried out to gather conclusive evidence for the above postulations. Whatever the mechanism(s) involved, the ability of seedling yarrow plants to survive in shaded environments appears to be an important characteristic which enables them to be present and survive in pastures (Fenner, 1978), lawns (Levy, 1931), cereal crops (Hilgendorf and Calder, 1952) and in *Pisum sativum, phaseolus vulgaris* and *Trifolium repens* seed crops (Bourdôt, White and Field, 1979; Bourdôt and Butler, 1981).

Though the seedling yarrow plants have the ability to survive in shaded habitats, their total dry weight was significantly less than at full daylight (Table 3.4). The total dry weight of the plants growing at 46.8%, 23.7% and 6.4% daylight was 61%, 45% and 5% respectively, of the dry weight of the plant in full daylight, after 23 weeks of growth. The decrease in the dry weight of the root, rhizome, leaf, stem and capitula fractions all contributed to the decline in the total dry weight of these plants (Table 3.4). Similar trends in the growth of other plants, in response to shading, have been reported: e.g., *Bromus inermis* (Watkins, 1940), *Lolium perenne*,

Dactylus glomerata, Trifolium repens, and *T. subterranean* (Mitchell, 1954), *Sorghum halepense* (McWhorter and Jordan, 1976), *Achillea millefolium* (Bourdôt, 1980), *Imperata cylindrica* (Patterson, 1980), and *Cyperus rotandus* and *C. esculentus* (Patterson, 1982). However, in Bourdôt's experiment, which was concluded after 4 weeks of introducing the yarrow seedlings to different shade levels, the effect of different light intensities on the dry weight of the rhizome and capitula fractions were not evaluated. Fenner (1978) found that yarrow plants growing at 6.8% full daylight produced only 7% dry matter as compared to plants growing in full daylight for the same length of time. This is in close agreement with the finding in the present study (Table 3.4).

Bourdôt (1980) found that the net assimilation rate (NAR) of seedling yarrow plants decreased at a faster rate than the corresponding increase in its leaf area ratio (LAR) when they were shaded, leading to the reduction in its relative growth rate (RGR). These physiological responses, according to the definition of Blackman and Wilson (1951b), are typical of a 'sun-loving' plant. The inability of changes in LAR to adequately compensate for the declining NAR appears to be the reason for the reduction in total dry weight of individually growing yarrow plants, when they are shaded.

The proportion of the total biomass allocated to the root and stem fractions of the seedling yarrow plants declined with shading, while the converse was true for the leaf fraction (Table 3.5). There was a 48%, 95% and 219% increase in the proportion of total biomass allocated to the leaves at 46.8%, 23.7% and 6.4% total light availability, respectively, compared to the allocation at full daylight. Similar trends in biomass allocation to the root, stem and leaf fractions can be inferred from the work carried out by Bourdôt (1980) on the effect of shade on seedling yarrow. These trends indicate that as the light availability to individually growing yarrow plants declined, their non-reproductive effort becomes

positiviely concentrated towards the leaf component, at the expense of the stem and root components. Bourdôt (1980) found that the leaf area of yarrow plants growing at 46.8% and 23.7% full daylight was greater than in plants in full daylight. Thus, the higher proportion of total biomass allocation to the leaves, when the plants are shaded, appears to be an effort towards providing a larger leaf area so as to intercept the maximum amount of solar radiation from an already depleted source. The marked reduction in the proportion of biomass allocated to the stems at 6.4% daylight (Table 3.5), compared to the other light intensities, was mainly due to the absence of flower stem production at this light level (Table 3.1).

Apart from the retardation of the growth and development of the non-reproductive components of seedling yarrow plants, increasing levels of shade decreased the sexual reproduction capacity of the plant (Tables 3.1, 3.2). Compared to the plants growing in full daylight, at 48.6 and 23.7% of full daylight, there was a 2 and 3 weeks delay, respectively, in the appearance of flower stems. A light intensity of 6.4% full daylight was not sufficient for the sexual phase of development to be initiated (Section 3.3.2.1). In many plant species, the initiation of flowering has been shown to be very sensitive to various environmental factors like photoperiod, temperature, mineral nutrients, etc. (Evans, 1969). Whatley and Whatley (1980) stated that apart from the photoperiod, the intensity and quality of the light available to the plants are important factors in the induction of the flowering response. In the present study, all plants received the same duration of light, quality of light (refer Section 3.2.1.2), and temperature (Appendix 5). The mineral nutrient availability to the plants should not have varied as the same soil was present in all treatments; the soil in all treatments was maintained at field capacity at all times. The sheltering effects and the possible higher humidity levels under the shades could not easily be measured, but may have caused some variations in the environment to plants growing under shade, compared to those in the open. However,

these effects may have been slight, as the 10 cm gap between the soil surface and the bottom edge of the shade houses and the mesh-like nature of the shade cloth would have allowed good air movement (refer Section 3.2.1.2). Thus, the major environmental factor which varied was the intensity of light received by the yarrow plants, and it appears to significantly affect the time and ability of these plants to flower. Bourdôt (1980) found that seedling yarrow plants at 100%, 46.8% 23.7% and 6.4% of full daylight flowered 9 weeks after emergence. The flowering of these plants, 4 weeks earlier than in the present study (refer Section 3.3.2.1), may have been due to the restriction of the growth of their roots in the smaller containers of 4 *l* capacity. The pretreatment of his plants for 5 weeks, before they were subjected to the lowest shade level (i.e., 6.4% full daylight availability) (refer Section 3.1), may have satisfied their light requirement for flowering. However, the exposure of yarrow seedlings to 3 weeks of full daylight, before reducing the light available to them to 6.4% of full daylight (refer Section 3.2.1.2), was not sufficient to induce flowering (refer Section 3.3.2.1).

With increasing levels of shading, the number of flower stems, capitula, and seeds per capitulum of seedling yarrow plants declined, leading to a markedly reduced seed output per plant (Table 3.1). Similar findings have been reported for other herbaceous species, including *Portulaca oleracea* (Noguchi and Nakayama, 1978a) and *Cyperus rotandus* and *C. esculentus* (Sendoya and de Dok, 1975; Keeley and Thullen, 1978). It can be argued that the shade houses would have prevented the cross pollination of the yarrow flowers and could have been an additional factor contributing to the reduced seed output of these plants, which are essentially self-sterile (Weijer, 1952; Warwick and Briggs, 1979). However, Dipterans, which usually pollinate these flowers, were present on these inflorescences in abundance. Therefore, effective cross pollination could have occurred in mature yarrow flowers.

The changes in vegetative reproductive effort of seedling yarrow plants, as they were increasingly shaded, were similar to those for sexual reproduction. The numbers of rhizomes and rhizome buds and their length declined markedly as the plants received less light (Table 3.2). However, unlike the situation for sexual reproduction (Table 3.1), vegetative reproduction continued even at 6.4% of full daylight, though at a very much reduced level compared to other light intensities (Table 3.2). The reduction in rhizome number and length resulted in the decrease in their total weight (Table 3.4). The above findings are similar to the effect of shade on the rhizome component of other herbaceous species, including *Sorghum halepense* (McWhorter and Jordan, 1976), *Imperata cylindrica* (Patterson, 1980), and *Cyperus rotandus* and *C. esculentus* (Patterson, 1982).

Bostock and Benton (1979) found that when individual seedling yarrow plants were grown in 14 cm plastic pots, 21.5% of the total biomass of the plants that flower in full daylight was allocated to the capitula while 26% was allocated to the rhizomes. However, Abrahamson (1979) stated that in field populations of yarrow, the percentages of total biomass allocated to subterranean tissues (i.e., roots and rhizomes), stem, leaf, and floral components were 34%, 29%, 21% and 15%, respectively. In the present study, individual seedling yarrow plants growing in full daylight in the field allocated approximately 17%, 21%, 21%, 27% and 14% of their total biomass to the root, rhizome, leaf, stem, and capitula fractions of the plant, respectively (Table 3.5). These findings are in close agreement with those of Abrahamson (1979). The higher allocation of total biomass to the capitula fraction in Bostock and Benton's (1979) work may have been due to the artificial restriction of the subterranean parts of the plants growing in pots of limited volume. In yarrow, a greater proportion of the biomass was partitioned to the vegetative reproduction components (i.e., the rhizomes) as compared to the sexual components (i.e., the capitula) (Tables 3.5, 3.6). But a comparison of the numbers of each type of reproductive

propagule produced revealed that substantially more seeds were produced than rhizome buds at 100% and 46.8% daylight (Tables 3.1, 3.2); the ratios of seed to buds at these light intensities were 25:1 and 20:1, respectively (Table 3.3). This is understandable as the risks involved in successfully establishing a seedling plant are far greater than when a ramet produces a plant vegetatively. The capital reserves in seeds are low compared to rhizomes (Appendix 6, Table 3.4). These seeds need to germinate on or near the soil surface and the resulting seedlings have to become self-supporting within a short period of time. In such a situation, the chances of mortality of seedlings is high. The converse is true for shoots arising from rhizome buds. Therefore, the yarrow plant has to 'wastefully' allocate energy towards the production of a large number of genets and thus increase the chances of successfully establishing at least a few seedling plants.

When the yarrow plants were increasingly shaded, the proportion of the total biomass partitioned to the rhizomes and capitula fractions declined (Table 3.5). At 23.7% of full daylight, 47% of dry matter was present in the capitula when compared to the dry weight of the rhizomes (derived from Table 3.6); at 6.4% of full daylight, the plants total reproductive effort was towards rhizome production (Table 3.5) and 12% of the total biomass was allocated for this purpose. Therefore, with decreasing light availability, the reproductive effort of yarrow plants was increasingly directed towards vegetative reproduction.

The present study shows that seedling yarrow plants are essentially 'sun-loving' plants which have the ability to survive at very low light levels. At lower light intensities, there is a consistantly greater biomass allocation towards vegetative reproduction in preference to sexual reproduction.

However, when seedling yarrow populations grow in association with other species, the level of shading and the quality of light available to

the yarrow plants will vary with time. Other types of competitive and/or non-competitive interference may also occur in such associations. The studies that follow enabled the evaluation of the survival, growth and development, and the reproductive effort of yarrow plants growing in association with crops.

CHAPTER 4

THE GROWTH AND DEVELOPMENT OF SEEDLING YARROW IN ASSOCIATION WITH A BARLEY OR PEA CROP AND SOME CHANGES THAT OCCUR AFTER CROP HARVEST

4.1 INTRODUCTION

In nature and under most agricultural situations, plants, whether they be a mixture of different species or of the same species, grow close to one another. The presence of neighbouring plants leads to changes in the growth and development of individual plants in the community (Clements *et al.*, 1929; Aspinall and Milthorpe, 1959; Holliday, 1960; Donald, 1963) and the degree of change that occurs varies with the proximity of the individuals to each other (Hodgson and Blackman, 1956; Lang *et al.*, 1956; Harper, 1961). Milthorpe (1961) stated that the degree of proximity of plants is a resultant of their spacing and size, the latter being determined by their initial seed reserves, their relative growth rate (RGR), and the time period for which they have been growing.

4.1.1 Growth Factors

Plants require the following basic factors; light, water, nutrients, oxygen, and carbon dioxide for growth. When growing in proximity to each other, plants modify both their soil and aerial micro-environments and this in turn influences their further growth and development. Light, water and nutrients have been recognized to be most commonly in short supply to plants growing together (Clements *et al.*, 1929; Donald, 1963; Rhodes, 1970b; Haynes, 1980). Carbon dioxide and oxygen supplies may also be inadequate, under special circumstances, to meet the demands of all the neighbouring

plants (Donald, 1963; Haynes, 1980). However, Monteith and Szeicz (1960) stated that the carbon dioxide within a plant community growing in the field is never depleted to a level where it can cause a retardation in the growth of plants. Some workers consider that the inadequacy of physical space can also lead to the suppression of plant growth and development (e.g., Harper, 1977; Haynes, 1980), while other workers (e.g., Clements *et al.*, 1929; Donald, 1963) state that the struggle for physical space between neighbouring plants is extremely rare. Further studies, where light, carbon dioxide, oxygen, temperature, water and nutrients are made available in excess of the needs of all individuals in a plant community grown at different densities, would show whether physical space is a factor which affects plant growth and development.

4.1.2 Terminology

The term 'competition' has been used to describe the biological and physical processes which influence the growth of plants at different or all stages of their development. Clements *et al.* (1929) defined competition as the phenomenon which takes place when the immediate supply of a single essential factor falls below the total demand of all the individual plants. Later definitions by De Wit and coworkers tend to confuse the issue (De Wit, 1960; De Wit and Van den Bergh, 1965; De Wit *et al.*, 1966). Milthorpe (1961) defined competition more broadly than Clements and coworkers, and stated that the term should include "those events leading to the retardation in growth of a plant when in association with other plants". Harper (1961) indicated that there was much controversy about the exact meaning of the word 'competition' and proposed the use of the term 'plant interference' to describe the long- and short-term hardships caused by the proximity of neighbouring plants. However, the word 'hardship' seems to cover only the detrimental facet of interactions among plants. The definition of 'plant

interference' as "the response of an individual plant or species to its total environment as this is modified by the presence and/or growth of other individuals or species" (Hall, 1974a) seems preferable as it accounts for both the beneficial (e.g. nitrogen fixed by a legume becoming available to an associated non-leguminous species) and detrimental influence of one plant or species on the other. Another term which embraces all mutual influences of plants growing together is 'neighbour effects' (Trenbath, 1974). However, Hall (1974a) suggested the use of the terms 'competitive interference' and 'non-competitive interference' to describe the phenomena which occur in plants when the immediate supply of one or more of the essential growth factors falls below the total demand of all the individual plants or due to any other processes which influence their growth, respectively.

4.1.3 Nature of Plant Interference

Competitive and/or non-competitive interference may occur due to the interaction of plants of different species (interspecific) and different cultivars/genotypes or of the same genotype (intraspecific) (Donald, 1951; Litav and Seligman, 1969; Rhodes, 1970a; Eagles, 1972). In mixed plant communities, which would include most natural habitats, mixed pastures, and mixed crops, both inter- and intra-specific interference can occur; in monocultural stands, free of weeds, only intra-specific interference is possible.

The shoot systems of neighbouring plants interfere with each other primarily for light (competitive interference). In a mixed plant community, the most successful component will usually be the one with a larger leaf area, high in the canopy, where it will capture most of the light and shade the shorter components (Black, 1958; Iwaki, 1959; Stern and Donald, 1962; Williams *et al.*, 1978). Several studies have indicated the importance of interference for light among pasture species (Black, 1957; Donald, 1951;

Stern and Donald, 1962) and crops (Pendleton and Seif, 1962; Willey and Osiru, 1972; Williams *et al.*, 1978).

The interference between the root systems of plants has been less carefully studied than shoot interference. Root interference is usually for nutrients and/or water (competitive interference) (Welbank, 1961; Donald, 1963). Allelochemicals released to the soil from living leaves (McPherson and Muller, 1969; del Moral and Muller, 1969 ; Groner, 1974; Trenbath, 1976), living roots (Hirano and Morioka, 1964; Webb *et al.*, 1967; Putnam and Duke, 1974), or dead and decaying plant parts (Welbank, 1961; Kimber, 1973) have also been reported as interfering with plant growth (non-competitive interference). However, it is difficult or impossible to prove conclusively that true allelopathy is occurring under field conditions (McPherson and Muller, 1969).

Several workers have attempted to isolate shoot and root interference (e.g., Donald, 1958; Aspinall, 1960; Caplenor, 1964; Schreiber, 1967; King, 1971; Snaydon, 1971; Eagles, 1972; Litav and Isti, 1974;). Except Schreiber, all these other workers showed that root interference was more intense and started earlier than shoot interference. This is possibly due to the root systems extending and intermingling before their shoot systems shade each other (Mann and Barnes, 1947; Donald, 1958; Milthorpe, 1961; King, 1971) and/or the soil factors more commonly limit the growth of plants than does light.

Bray (1954) concluded that root interference between plants is much greater for relatively mobile nutrients. Several workers have reported that plants interfere with each other in order to acquire adequate supplies of nitrogen (e.g., Blackman and Templeman, 1938; Donald, 1958; Nieto and Staniforth, 1961; Welbank, 1961, 1964; Litav and Wolovitch, 1971), potassium (e.g., Blackman and Templeman, 1938; Blaser and Brady, 1950; Mouat and Walker, 1959; Hall, 1974b), phosphorus (e.g., Mouat and Walker, 1959; Snaydon, 1971; Jackman and Mouat, 1972a, b) and sulphur (e.g., Walker and Adams,

1958). However, the relative importance of various nutrients will depend on soil type, plant species involved, and the experimental technique used.

Donald (1963) stated that interference between plants for water generally occurs together with interference for growth factors such as nitrogen and light. The efficiency with which available water is used by pasture plants generally increases when fertilizers are applied. The success of a plant or plant species in acquiring adequate supplies of available water depends on the rate and completeness with which it uses the soil water supply. Several workers have reported the interference between plants for water (e.g., Jackman and Mouat, 1972b; Evans, 1978).

A number of workers have shown that the effects of simultaneous interference of soil and aerial factors in plant associations were greater than when the factors acted separately and independent of each other (e.g., Donald, 1958; Aspinall, 1960; Snaydon, 1971). Plants growing in natural habitats and those cultivated in the field are likely to experience interference of both soil and aerial factors during growth. The present knowledge of the inter-relations between the different growth factors is very limited and it is difficult to state categorically whether the factors interact with each other or that their effects are merely cumulative (Hall, 1974a). De Wit (1960) stated that the subdivision of plant interference (e.g. interference for light, water, and nutrients, etc.) is " ... not necessary, always inaccurate and therefore inadvisable". However, other workers (e.g. Snaydon, 1971; Eagles, 1972; Hall, 1974a, b) believe that though investigating the effects of an isolated factor or a combination of them on the growth development of individual plants or species (growing in association) may not reveal the true nature of the mutual influences occurring among plants in the field, the quantification of the effects of these factors may lead to a better understanding of the processes governing mutual influences between plants and indicate how they may be manipulated to advantage.

4.1.4 Plant Characteristics Which Determine Success in Situations of Interference

Sakai (1961) attempted to define which morphological characters determine the success of plants or species when in intra-specific and/or inter-specific interference. He looked at the correlation between morphological characters, such as plant height and plant weight, of a number of cereals and their success in competitive interference ('competitive ability') and concluded that no significant correlation existed. However, seed and seedling characters like size of seed (i.e., embryonic capital) (Black, 1957, 1958; Aspinall and Milthorpe, 1959), seed polymorphism (Harper, 1964), relative rate of emergence (Harper, 1961; Haynes, 1980), and seedling vigour (Blaser *et al.*, 1956; Laskey and Wakefield, 1978); shoot characteristics like canopy height (Iwaki, 1959; Black, 1960; Donald, 1963; Harper, 1964), leaf area (Norman *et al.*, 1971; Haynes, 1980), leaf architecture (Acock *et al.*, 1970; Haynes, 1980), leaf angle (Brougham, 1958), leaves with C4 photosynthetic pathway (Black *et al.*, 1969), leaf transmissivity (Saeki, 1960), rate of stem elongation in response to shading (Williams, 1964), and shade tolerance (Langer, 1973); and root characteristics like rate of penetration of soil (Harris, 1967; McCowan and Williams, 1968), high root density (Andrews and Newman, 1970), high root/shoot ratio (Idris and Milthorpe, 1966), high root length/root weight ratio (Harris, 1967; Olsen and Kemper, 1968), long root hairs (Drew and Nye, 1969; Barley, 1970), higher uptake of nutrients (Idris and Milthorpe, 1966; Bowen, 1973), earlier uptake of water (Cohen, 1970; Troughton, 1974), lower root cation exchange capacity (Gray *et al.*, 1953; Mouat and Walker, 1959b), and symbiotic nitrogen fixation (Vallis, 1978; Haynes, 1980) have been shown to endow success to some plant species over others, when growing in association with each other.

Sakai (1955) postulated that the success in 'competitive ability' is genetically based and is not easily or readily definable in terms of phenotypic behaviour. However, Welbank (1963), quoting Harper, disagrees with

Sakai's postulation and states that "the concept of an innate quality of competitiveness as a property of a species and not an association of the species with any particular competitor, may have no real meaning. If it were valid, the order of competitive effect of several species on an indicator species ought not to be changed by substituting a different indicator". He continues to say that there are many instances where the order of effects of two species might be reversed and therefore it is not possible to consider the 'competitive ability' of one species without reference to the particular species 'competed' against. Furthermore, because of the large number of morphological and physiological characters which can determine the 'competitive ability' of different species, it is unlikely that any uniform pattern of heritability would be present. Referring to the work of Oka, Donald (1963) stated that "when examined as a genetic character, 'competitive ability' has shown very low heritability".

4.1.5 Approaches to the Study of Plant Interference

An agronomist's approach to the study of plant interference can be conveniently divided into the description of changes that occur in growth and development of plant communities and/or individual plants and attempts to relate these changes to the variations in the aerial and soil environment where the plants are growing. Several workers have described the vegetative and reproductive changes that occur when neighbouring plants interfere with each other by acquiring a disproportionate share of limited growth factors (e.g., Donald, 1958; Aspinall and Milthorpe, 1959; Aspinall, 1960; Harper, 1961; Singh *et al.*, 1967; Snaydon, 1971) or by the production of allelochemicals (Webb *et al.*, 1967; Putnam and Duke, 1974). However, the presence of allelopathy cannot be conclusively established under field conditions (McPherson and Muller, 1969; Trenbath, 1976). The techniques used to study plant interference can be broadly categorized as: firstly, those which describe the effects of plant interference over time (commonly

known as 'growth analysis') where some of the physiological changes that are responsible for the observed effects become apparent, and secondly, those based on the principles and procedures essentially developed by De Wit (1960), where competitive and non-competitive interference can be distinguished and quantified (e.g., Hall, 1974a, b; Ivens and Mlowe, 1980).

In the following study, growth analysis techniques were used to evaluate the nature of the physiological changes that occur in populations of seedling yarrow when in association with certain specific crops and their effects on the growth of yarrow. Growth analysis is a technique by which the dynamics of photosynthetic production can be followed through time by measuring the changes that occur in the size of the assimilatory apparatus and production of dry matter. Kvet *et al.* (1971) stated that it could be used to investigate ecological phenomena such as interference among species. In studies of plant growth analysis, either a 'classical' approach or a 'functional' approach can be adopted. In the 'classical' approach, the changes that occur in plants (i.e., either single plants or plant populations) are followed through a series of relatively infrequent, large harvests. In the 'functional' approach, the harvests are comparatively smaller but taken more frequently. Unlike in the 'classical' approach, where the short-term fluctuation in the growth and development in plants can be obtained (i.e., the changes in growth between two adjacent harvests), in the 'functional' approach the general trends of these plant characteristics over the entire period of experimentation can be studied by fitting smooth 'curves of best fit' to all the raw data. In the following study, where the effects of barley (*Hordeum vulgare*) and pea (*Pisum sativum*) plants on the growth and development of seedling yarrow needed to be evaluated both during the period of crop growth and after the crops were harvested, a 'functional' approach was considered to be more appropriate. Details of 'functional' approach are given in Appendix 8.

Previous observations showed that yarrow was not a problem weed in barley crops even when they were sown in fields which had a history of yarrow

infestation (Kannangara, unpublished). However, the converse was true when pea crops were cultivated on such fields (Bourdôt, White and Field, 1979). As these crops facilitated two extremes of behaviour of yarrow plants growing in association with them, they were selected for the following study.

4.2 MATERIALS AND METHODS

4.2.1 Experimental Site, Design and Treatments

The experimental site situated at Lincoln College, New Zealand, had Wakanui silt loam soil that was free draining. It had been under lucerne (*Medicago sativa* L.) since 1973 and had no previous history of the presence of yarrow. The land was cultivated in the first week of September 1979, to get a seed bed of good tilth. The experimental plots were 6 x 3 m, and arranged in a fully randomized block design with 1 m between adjacent plots. The treatments were as follows:

1. Pure stand of yarrow.
2. Yarrow in association with barley plants (*Hordeum vulgare* cv. Zephyr).
3. Yarrow in association with pea plants (*Pisum sativum* cv. Huka).
4. Pure stand of barley.
5. Pure stand of peas.

Each treatment was replicated 6 times.

4.2.2 Soil Sterilization

The soil in each plot was fumigated to kill the resident seed and other plant propagules. Only seedling plants of yarrow, barley and peas established after soil sterilization were allowed to grow. The few plants

of shepherd's purse (*Capsella bursa-pastoris* (L.) (Medic.), fathen (*Chenopodium album* agg.), and white clover (*Trifolium repens* L.) that emerged from time to time were removed by hand before they reached the two true leaf stage.

Three plastic containers (0.5 ℓ capacity) were placed at the middle of each plot at regular intervals along its length. One end of a gas applicator tube was directed into each container, while the other end, where the gas (fumigant) cans fit, was outside the plot. The plot was covered with a sheet of black horticultural grade polythene (14 x 4 m); liver pails were placed on the plot at regular intervals before covering to ensure that the sheet was not in contact with the soil surface. The edges of the sheet were buried in a 15 cm trench dug around the plot so as to 'seal' the area under the polythene sheet.

When the soil temperature of the plot at 10 cm depth was 15^{o}C (i.e., on 15 September 1979), methyl bromide gas was applied via the applicator tubes; "Dowfume MC-2 Penetrating Fumigant" containing 980 g kg^{-1} methyl bromide and 20 g kg^{-1} chloropicrin was applied at the rate of 5, 0.45 kg cans per 18 m^{2} plot. The applicator tubes were drawn out immediately after delivery of the gas and more soil was added along the edges of the polythene sheet and compacted to prevent the escape of the fumigant. One week later (i.e., on 22 September 1979), the polythene sheet was removed and the soil allowed to ventilate for another 7 days before sowing the trial.

4.2.3 Density of Yarrow

The density of the yarrow stand to be established was determined after plant counts were made on natural stands of seedling yarrow. Ten 0.12 m^{2} quadrant counts were taken at random, on 15 September 1979, from fields close to the experimental site. The mean number of plants per unit area was taken as the density to be established (i.e., 250 plants m^{-2}).

4.2.4 Seed Material

Sun dried yarrow seed heads were collected in March 1979 from naturally growing populations of yarrow found close to the experimental site. They were lightly rubbed on a wire mesh to dislodge the seed and the chaff and light seed were blown away by directing a regulated air flow. The cleaned seed was placed in a black polythene bag and stored at room temperature until used in the experiment. Certified barley and pea seed were used.

Laboratory germination tests were carried out in accordance with the recommendations of the I.S.T.A. (1976), where imbibed yarrow seed were supplied with 20 - 30°C alternating temperature and 8 h light day^{-1} (3875 lux intensity; refer Chapter 2). The imbibed barley and pea seed were incubated at 20°C in diffuse light. Mean germination percentages of 98 (S.E. 1.4), 96 (S.E. 2.0) and 98 (S.E. 2.0) were obtained for yarrow, barley and peas, respectively, after 21 days incubation.

4.2.5 Establishment of Plants

Barley and pea seed were drilled with a Stanhay precision drill into the appropriate plots in rows spaced 15 cm apart; the seeds were sown to a depth of approximately 2 cm at the rate of 150 and 300 kg ha^{-1}, respectively.

The amount of yarrow seed required for each plot (i.e., 250 seeds m^{-2} assuming complete germination) was worked out according to a previously calculated relationship between seed weight and seed number (Appendix 6); forty per cent more seed was added as an allowance for possible lower field germination, giving 1.014 g seed per 18 m^2 plot. The yarrow seed for each plot was thoroughly mixed in 4 ℓ of slightly moist river sand and evenly broadcast by hand on 29 September 1979; a similar quantity of sand was broadcast on each plot that did not receive yarrow seed. Calm weather prevailed during this operation. A light irrigation was carried out on the following day using an

oscillating irrigation spray line; no further irrigations were carried out. As the land had been under lucerne for the 7 previous years, the fertility of the soil was high. Therefore, no fertilizer was applied to the plots.

4.2.6 Sampling and Measurement Procedures

Three-weekly samples were taken, starting from 26 October 1979, over a period of 15 weeks after seedling emergence; a further 4 samplings were carried out at 6 weekly intervals, after the barley and pea crops were harvested. On the day of sampling, the total amount of photosynthetically active radiation (PAR) available 1 m above the crops and pure stand of yarrow and at the surface of the yarrow populations in association with the crops were measured. A Licor C-275 quantum sensor was levelled with a spirit level before the measurements were made; the measurements are given in Appendix 7 as a percentage of the total available PAR.

Plants within a randomly selected 0.12 m^2 quadrant were removed from each treatment by digging the soil to a depth of 20 cm. Care was taken to collect all rhizome material. A 30 cm border strip was left around each sampling area. Individual samples were washed in running water to remove the soil adhering to the subterranean parts.[#]

At each sampling, the number of yarrow plants within the quadrat area was counted. The root fraction of each sample was discarded. The yarrow plants were fractionated into green and dead leaves, stems, and rhizomes; the crop plants were fractionated into leaves (i.e., lamina in barley plants; lamina + petioles + auricles in pea plants) and stems (inclusive of leaf sheaths in barley plants).

The areas of the green leaves were measured using a Licor model 3100 area meter. The separate plant fractions were oven dried at 80°C to a constant weight. At 15 weeks after seedling emergence, the machine-dressed seed yields of barley and pea crops were determined from 1 m^2 samples from their

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[#]Effective root nodules were present in the pea plants.

respective plots. The barley crop was machine-harvested, leaving the stubble to a height of about 10 cm; the pea crop was harvested by hand, leaving only the root fraction in the soil.

Apart from the above detailed sampling and measurement procedures, further samplings were carried out at weekly intervals, from the time of yarrow seedling emergence in pure stands (i.e., from 5 October 1979), to record the developmental stages up to 21 weeks (Appendix 13).

4.2.7 Analytical Procedure

Separate and suitable mathematical functions, represented by smooth curves, were fitted to the total weight, leaf area, leaf weight, stem weight, and rhizome weight data of seedling yarrow recorded from 3 to 15 weeks after seedling emergence. An outline of the principles involved and the mathematical aspects of the technique used is given in Appendix 8. Similarly, curves were fitted to the total weight and leaf area data of barley and pea crops over the same period of time. Only the trends in total growth and rhizome growth of the three stands of yarrow, from 15 to 33 weeks after seedling emergence, were of specific interest in the current study. Therefore, curves were fitted only to the total weight and rhizome weight data of the yarrow, over this period. The respective relative growth rates were derived from the fitted functions. The specific leaf area, leaf weight ratio, leaf area ratio, and net assimilation rate of the different stands of yarrow, from 3 to 15 weeks after seedling emergence, was derived from their respective fitted functions.

4.3 RESULTS

SECTION I: Yarrow in Association with the Barley Crop and the Pea Crop

4.3.1 Plant Population

The first seedlings of barley, peas, and yarrow, emerged from the soil on 5 October 1979, one week after sowing. The majority of seedlings emerged during the following week, although there was continued emergence of a few yarrow seedling until the end of October 1979. The yarrow seedlings were uniformly distributed in their respective plots. The crop stands were even and had 146 and 90 plants m^{-2} of barley and peas, respectively. The 5th of October 1979 was considered as the first day of emergence of all seedlings and the base date for subsequent measurements.

The objective of establishing 250 plants of yarrow per m^2 was not realized, owing to its poor germination and establishment. Three weeks after seedling emergence (26 October 1979), the number of plants growing in association with the barley crop was significantly higher than in the pea crop and pure stand of yarrow (Table 4.1). However, from 6 weeks after seedling emergence, there was no significant difference in the populations of yarrow plants, either in association with the crops or in pure stands. There were approximately 82, 67, 55, and 58 plants m^{-2} at 6, 9, 12 and 15 weeks after seedling emergence respectively (Table 4.1). From 3 to 6 weeks after seedling emergence, the decrease in the density of the yarrow population in association with the barley crop was significantly higher than in the pea crop and in the pure stand of yarrow (Table 4.2).

4.3.2 Total Dry Weight

The dead leaf fraction of yarrow was included in the total weight measurements; the root fraction was excluded (Section 4.2.6). The changes

Table 4.1: Seedling yarrow plants present in the pure stand and in association with barley and pea crops. Each value is a mean of 6 replicates.

Sampling Date	Plants m^{-2}			$LSD_{0.05}$	C.V. (%)
	Yarrow (Pure Stand)	Yarrow in Barley Crop	Yarrow in Pea Crop		
26 October 1979	120.0	174.7	127.8	36.6	16.6
16 November 1979	76.7	84.2	83.8	7.6	14.3
7 December 1979	66.5	68.0	67.4	2.7	7.1
28 December 1979	54.8	56.8	54.3	3.6	6.7
18 January 1980	56.7	57.1	58.6	3.3	4.8

Table 4.2: The loss or gain* of seedling yarrow plants between adjacent sampling dates. Each value is a mean of 6 replicates.

Sampling Date	Plants m^{-2}			$LSD_{0.05}$	C.V. (%)
	Yarrow (Pure Stand)	Yarrow in Barley Crop	Yarrow in Pea Crop		
26 Octoer to 16 November 1979	46.7	94.1	42.0	42.4	16.9
16 November to 7 December 1979	10.8	18.4	16.4	13.4	12.7
7 December to 28 December 1979	12.2	11.3	13.3	2.2	8.2
28 December 1979 to 18 January 1980	-2.3	-1.3	-5.1	5.3	6.8

*The negative values indicate a gain.

in leaf weight (Fig. 4.5), stem weight (Fig. 4.7), and rhizome weight (Fig. 4.9) with time were reflected in the growth trends of $\log_e$ total weight (W) (Fig. 4.1). A cubic model adequately described the changes in W of the yarrow populations and barley crop while a quadratic model best described the changes in W of the pea crop; the observed mean values are given in Appendices 10 and 11. The fitted model for each crop was identical whether it was in pure stand or in association with yarrow.

From 6 weeks after seedling emergence W of yarrow in pure stand, in barley crop, and in pea crop, were significantly different[#] from each other (Fig. 4.1); the only exception being at 15 weeks after seedling emergence, when W of yarrow in the pure stand and in the pea crop were not statistically different. When comparing the effects of the two crops, the barley suppressed W of yarrow to a significantly greater extent than the peas. As the total weights of the crops increased (Fig. 4.1), the W of the yarrow populations in association with them were increasingly retarded. At 10 weeks after seedling emergence, the barley and pea crops flowered and from then onwards their leaf areas declined rapidly (Fig. 4.3). During this period, there was a marked increase in the W of the yarrow populations growing with the crops (Fig. 4.1).

The above described changes in W of yarrow populations in pure stand and with the crops were associated with differences in their respective relative growth rates (RGR) (Fig. 4.2). The RGR of the pure stand of yarrow, at 6 and 9 weeks after seedling emergence, was significantly higher than in the populations growing with the crops; at 3, 12 and 15 weeks after seedling emergence, the RGR of the yarrow in association with the pea crop was significantly greater than when barley plants were growing in association. The initial differences in RGR of these yarrow populations led to the marked divergence in W with time (Fig. 4.1). However, the rapid increase in RGR of yarrow in association with the pea crop from 10 weeks after seedling emerg-

[#]Indicated by the lack of overlapping of their confidence bands at each sampling date.

Fig. 4.1: Progress curves of total dry weight m^{-2}. The points are the observed means of the logarithms of total dry weight of: (a) seedling yarrow in pure stand and in association with the pea and barley crops, and (b) the pea and barley crops in association with the yarrow stand. The lines are the curves fitted to all individual samples. The bars are the confidence limits for the derived values (95% probability); they apply equally to all the curves in their respective sets. The curves for (a) and (b)(refer above) form different sets. As the fitted curve for each crop in association with yarrow is identical to its curve when growing in pure stand, only the former is presented in the figure.

(a)

▲ Pure stand of yarrow

$\text{Log}_e W = -7.062 + 1.77742t = 0.0445234t^2 - 0.000843519t^3$

■ Yarrow in pea crop

$\text{Log}_e W = -11.772 + 4.06657t - 0.4151274t^2 + 0.014446605t^3$

● Yarrow in barley crop

$\text{Log}_e W = -8.689 + 2.54608t - 0.2556595t^2 + 0.008748765t^3$

(b)

□ Pea crop in yarrow stand

$\text{Log}_e W = 0.270 + 1.09221t - 0.0477944t^2$

○ Barley crop in yarrow stand

$\text{Log}_e W = -1.776 + 2.89531t - 0.3371111t^2 + 0.013095679t^3$

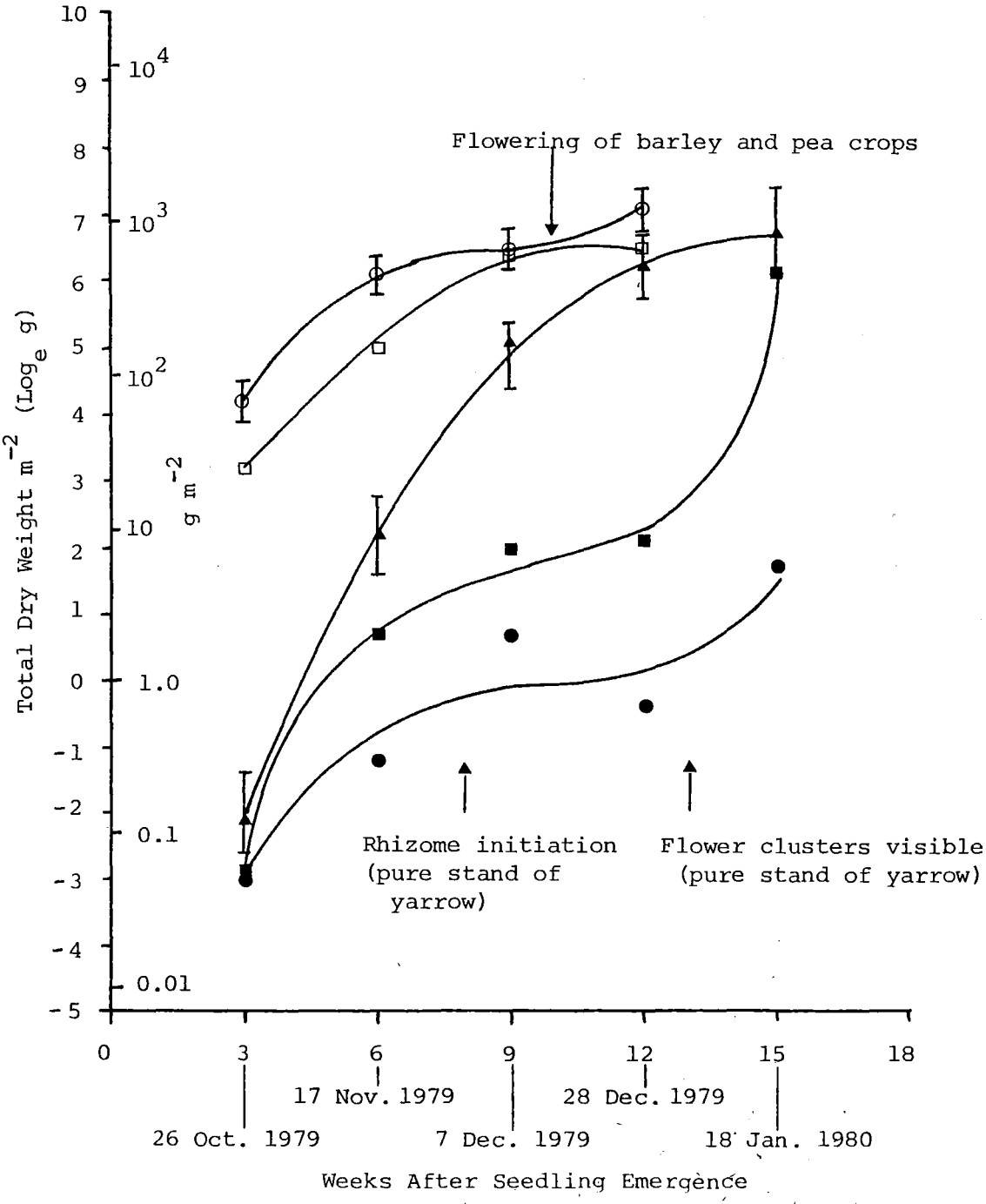


Fig. 4.2: Progress curves of relative growth rate of total dry weight of: (a) seedling yarrow in pure stand and in association with the pea and barley crop, and (b) the pea and barley crops in association with the yarrow stand, derived by differentiation of Fig. 4.1. The bars are the confidence limits for the derived values (95% probability); they apply equally to all the curves in their respective sets. The curves for (a) and (b) form different sets. As the derived curve for each crop in association with yarrow is identical to its curve when growing in pure stand, only the former is presented in the figure.

(a) ▲ Pure stand of yarrow.
■ Yarrow in pea crop.
● Yarrow in barley crop.

(b) ○ Barley crop in yarrow stand.
□ Pea crop in yarrow stand.

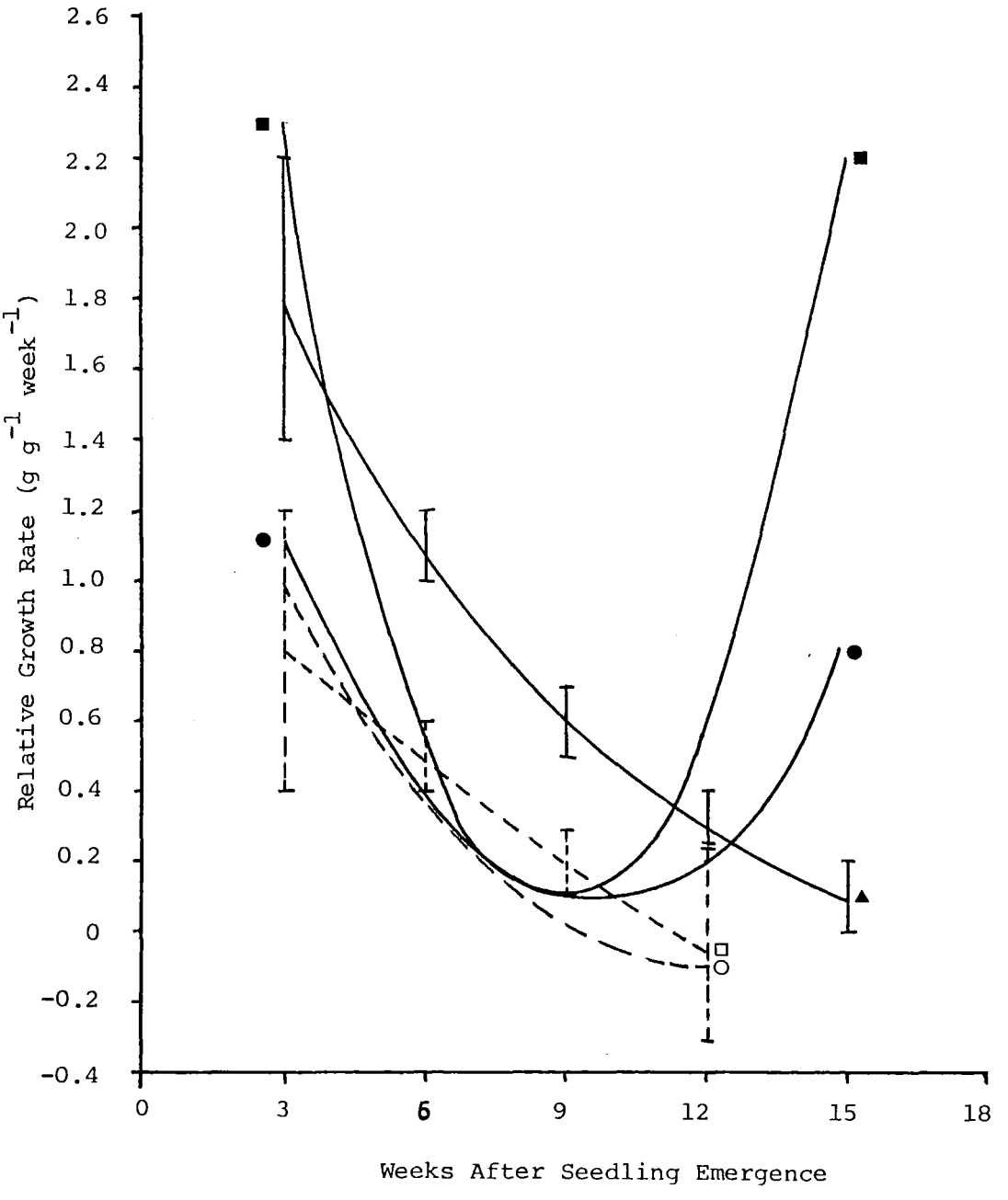


Figure 4.3: Progress curves of leaf area m^{-2}. The points are the observed means of the logarithms of total leaf area of: (a) seedling yarrow in pure stand and in association with the crops, and (b) the crops in association with yarrow. The lines are the curves fitted to all individual samples. The bars are the confidence limits for the derived values (95% probability); they apply equally to all curves in their respective sets. The curves for (a) and (b) form different sets. As the fitted curve for each crop in association with yarrow is identical to its curve when growing in pure stand, only the former is presented in the figure.

ence, compared to the continued decline in the RGR of the pure stand of yarrow (Fig. 4.2), enabled it to have a W which was not significantly different from the pure stand at crop harvest, 15 weeks after seedling emergence (Fig. 4.1). There was no difference in the RGR of the crops and they declined from 3 to 12 weeks after seedling emergence (Fig. 4.2).

4.3.3 Total Leaf Area

The changes with time of $\log_e$ leaf area (LA) was adequately explained by a cubic model; Figure 4.3 shows that the observed data (Appendices 10 and 11) fit the model extremely well. Even though the density of yarrow plants in the barley crop was much greater than in the pea crop and pure stand (Table 4.1), the leaf area of the three yarrow populations were similar at 3 weeks after seedling emergence (Fig. 4.3). The LA of the yarrow populations in the pea crop and pure stand increased with time. There was a decrease in the LA of yarrow growing with the barley crop from 3 to 9 weeks after seedling emergence; this was followed by a rapid increase in its LA when the LA of the barley crop fell below 1.2 m^2 m^{-2} (Fig. 4.3). A similar trend in the growth of LA of the yarrow population in the pea crop was evident from 9 weeks after seedling emergence when the LA of the pea crop declined. The increase in LA of the pure stand of yarrow was significantly greater than when it grew in association with the crops (indicated by the lack of overlapping of their confidence bands at each sampling date) (Fig. 4.3). The development of LA in yarrow was most retarded in the presence of the barley crop; it was significantly less than when the yarrow plants had pea plants as their neighbours.

The above-described differences in the LA of the three yarrow populations can be readily explained by examining their relative growth rates (RGR_A) (Fig. 4.4). Although the RGR_A in the pure stand of yarrow declined throughout, up to 9 weeks after seedling emergence it was significantly greater than in the yarrow populations in the barley and pea crops. Even

(a)

▲ Pure stand of yarrow

$\log_e LA = 2.521 + 0.19459t + 0.1217314t^2 - 0.006580556t^3$

■ Yarrow in pea crop

$\log_e LA = 2.385 + 0.69313t - 0.0461647t^2 + 0.001864506t^3$

● Yarrow in barley crop

$\log_e LA = 4.468 - 0.14649t - 0.0143202t^2 + 0.002262654t^3$

(b)

□ Pea crop in yarrow stand

$\log_e LA = 6.911 + 0.35644t + 0.0502945t^2 - 0.005017901t^3$

○ Barley crop in yarrow stand

$\log_e LA = 3.681 + 2.99264t - 0.3847333t^2 + 0.013673457t^3$

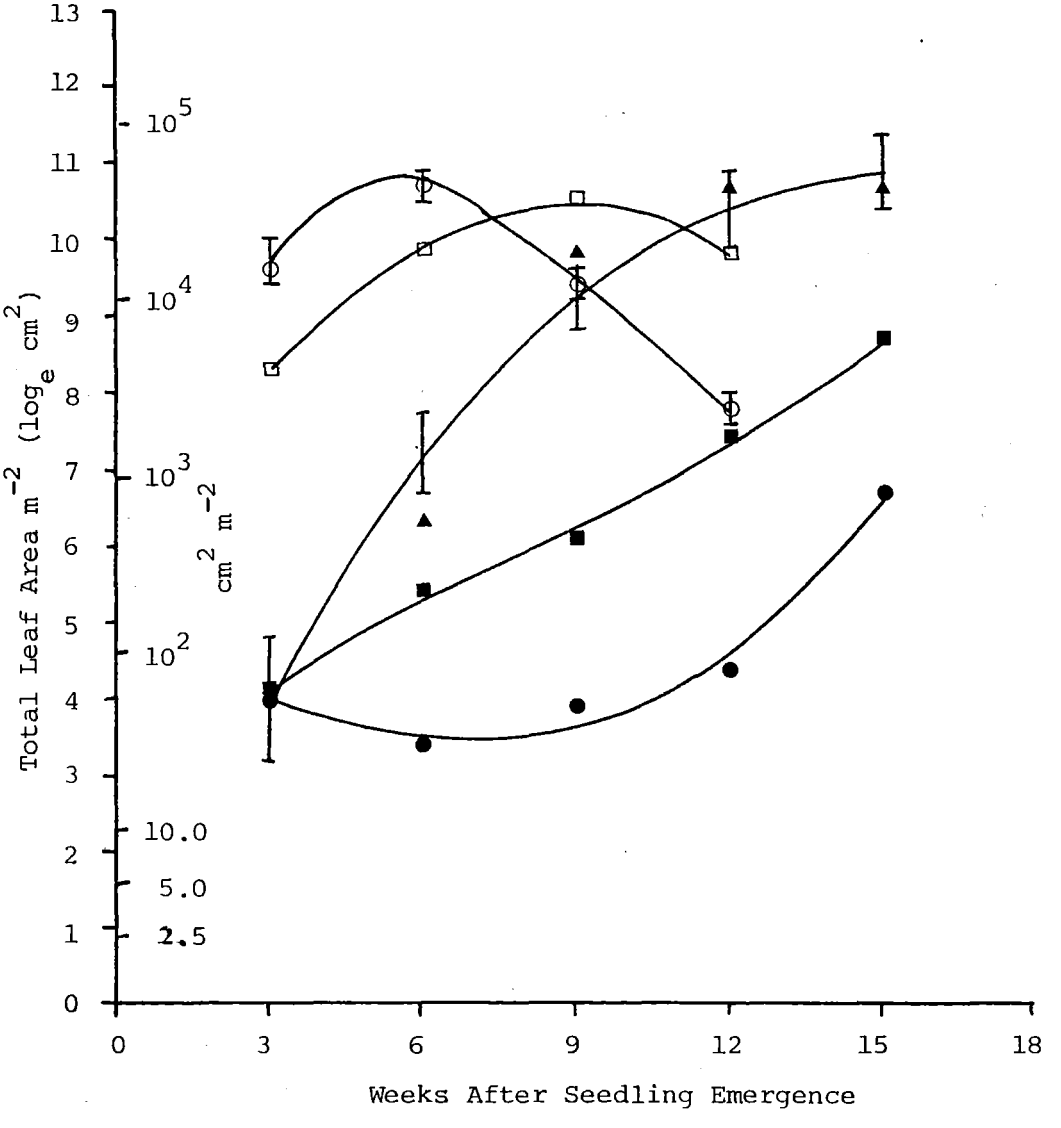


Figure 4.4: Progress curves of relative growth rate of leaf area of yarrow, derived by differentiation of the appropriate equations in Figure 4.3. The bars are the confidence limits of the derived values (95% probability); they apply equally to all curves.

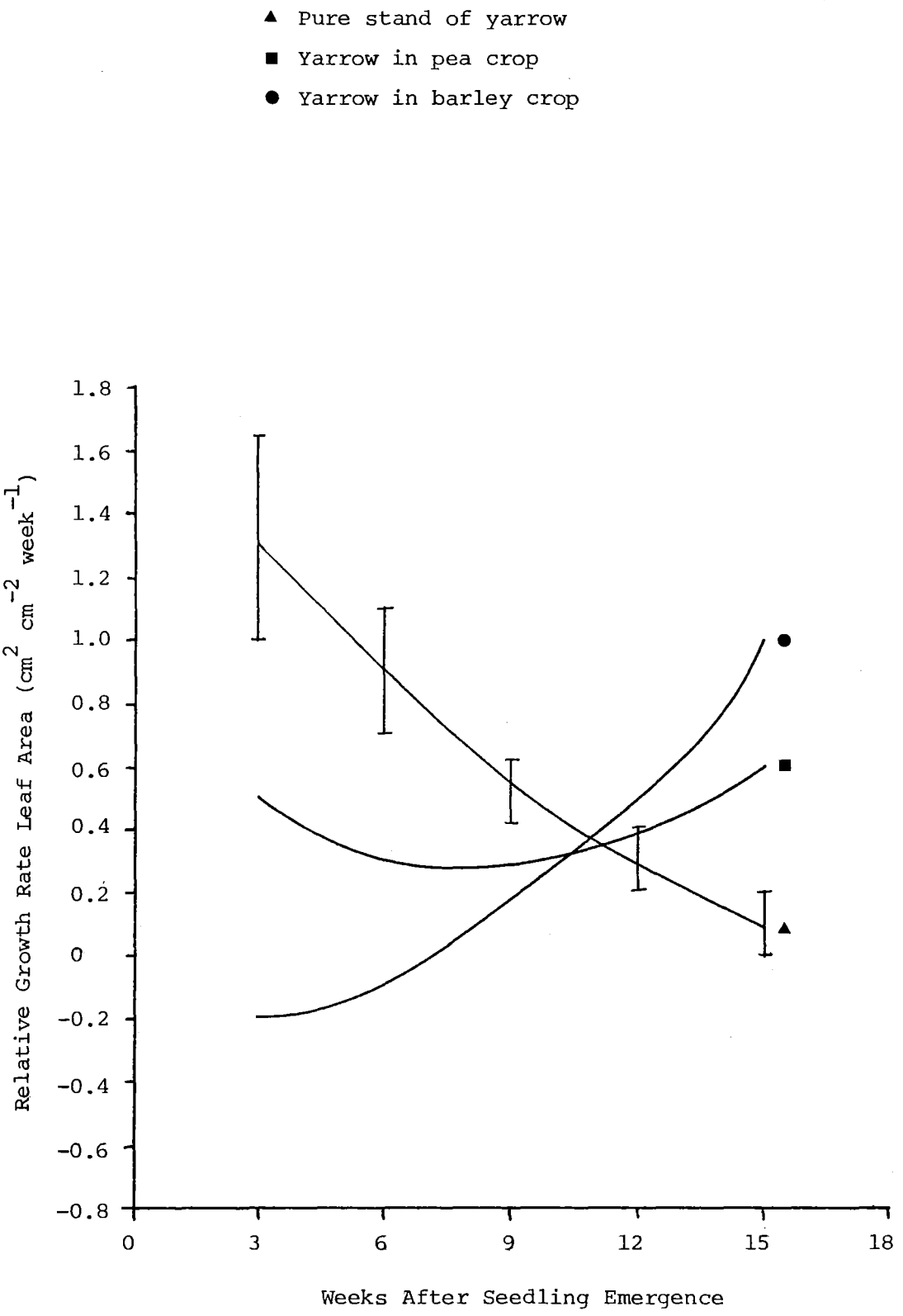

▲ Pure stand of yarrow
■ Yarrow in pea crop
● Yarrow in barley crop
Relative Growth Rate Leaf Area (cm^2 cm^{-2} week^{-1})
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
0
3
6
9
12
15
18
Weeks After Seedling Emergence

Figure 4.5: Progress curves of leaf dry weight m^{-2}. The points are the observed means of the logarithms of total leaf dry weight of seedling yarrow in pure stand and in association with pea and barley crops. The lines are the curves fitted to all individual samples. The bars are the confidence limits for the derived values (95% probability); they apply equally to all curves.

though the values for RGR_A of the yarrow populations in association with the crops were greater than in the pure stand from 12 weeks after seedling emergence, the initial advantage of a comparatively higher RGR_A enabled the pure stand of yarrow to have a significantly higher LA up to 15 weeks after seedling emergence (Fig. 4.3). Similar trends in RGR_A were evident between the yarrow populations in association with the barley and pea crops, with the latter being significantly higher than the former at 3 and 6 weeks after seedling emergence (Fig. 4.4); hence the yarrow stand in the pea crop had a higher LA compared to the yarrow population in the barley crop (Fig. 4.3).

4.3.4 Total Dry Weight of Green Leaves

A cubic model best described the change in $\log_e$ leaf weight (LW) with time (Fig. 4.5); observed mean values are given in Appendix 10. The LW of yarrow in pure stand and in association with the crops were similar at 3 weeks after seedling emergence and generally increased with time. Owing to a significantly higher relative growth rate of LW (RGR_{LW}) of the pure stand of yarrow from 6 to 9 weeks after seedling emergence (Fig. 4.6), its LW increased more rapidly than in the yarrow stands in the crops during this period. Even though the RGR_{LW} of the yarrow stands in association with the crops increased rapidly after 9 weeks from seedling emergence, while the RGR_{LW} of the pure stand of yarrow continued to decline, the LW of the pure stand remained significantly higher owing to the initial advantage of its higher RGR_{LW}. The LW of the yarrow populations in association with the barley and pea crops increased at a diminishing rate up to 9 weeks after seedling emergence (Fig. 4.5), owing to their declining RGR_{LW} (Fig. 4.6); from then onwards the steeply rising RGR_{LW} of these populations enabled them to exhibit rapid growth. The RGR_{LW} of the yarrow stand in the pea crop was consistently higher than for the yarrow population in association with the barley crop (Fig. 4.6) and thus the LW of the former

▲ Pure stand of yarrow

$\log_e LW = -15.146 + 4.20419t - 0.276537t^2 + 0.006021605t^3$

■ Yarrow in pea crop

$\log_e LW = -14.465 + 4.27386t - 0.4001710t^2 + 0.013239185t^3$

● Yarrow in barley crop

$\log_e LW = -14.389 + 4.33295t - 0.4446897t^2 + 0.015060494t^3$

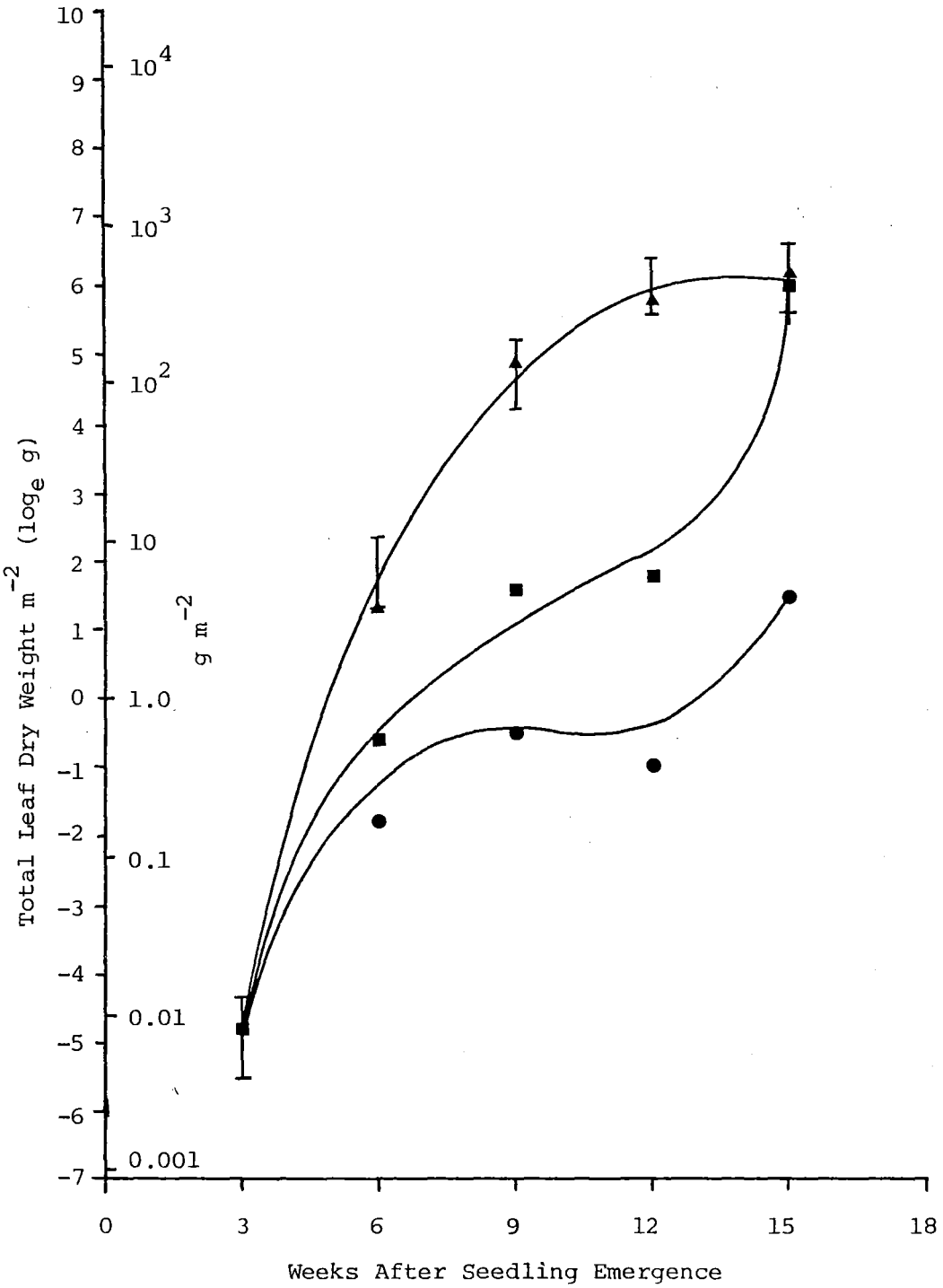


Figure 4.6: Progress curves of relative growth rate of leaf dry weight, derived by differentiation of Figure 4.5. The bars are the confidence limits of the fitted values (95% probability); they apply equally to all curves.

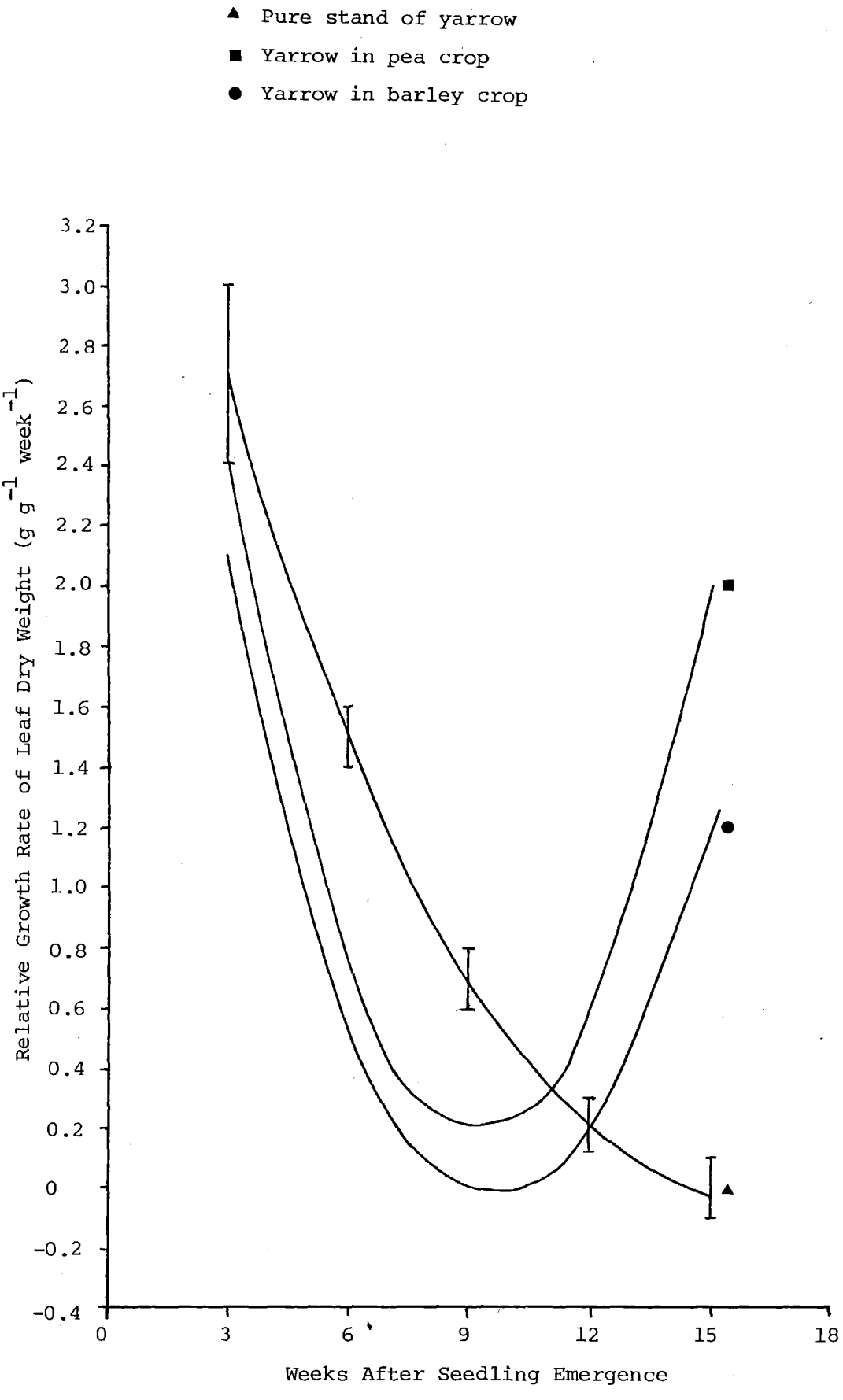

▲ Pure stand of yarrow
■ Yarrow in pea crop
● Yarrow in barley crop
Relative Growth Rate of Leaf Dry Weight (g g^{-1} week^{-1})
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
0
3
6
9
12
15
18
Weeks After Seedling Emergence

Figure 4.7: Progress curves of stem dry weight m^{-2}. The points are the observed means of the logarithms of total stem dry weight of seedling yarrow in pure stand and in association with the pea and barley crops. The lines are the curves fitted to all individual samples. The bars are the confidence limits for the derived values (95% probability); they apply equally to all curves.

yarrow stand was significantly greater than the latter (Fig. 4.5).

4.3.5 Total Stem Dry Weight

The $\log_e$ stem weight (SW) of yarrow in the pure stand and in association with the crops generally increased with time and a cubic model adequately described the changes (Fig. 4.7); the observed mean values are given in Appendix 10. From 9 weeks after seedling emergence, the SW of the pure stand of yarrow was significantly higher than the yarrow populations in the barley and pea crops. The growth in SW of yarrow in the pea crop was, however, suppressed to a significantly lesser extent than when barley plants were in association with the yarrow population. The significantly higher relative growth rate of SW (RGR_{SW}) of the pure stand of yarrow, compared to the yarrow populations in association with the crops, from 6 to 12 weeks after seedling emergence (Fig. 4.8), was responsible for the higher stem weight of yarrow in monoculture (Fig. 4.7).

The significantly higher RGR_{SW} of the yarrow stand in the pea crop, compared to the yarrow population in the barley crop, at 3, 6, and 15 weeks after seedling emergence (Fig. 4.8) enabled it to attain and maintain a higher SW than in the yarrow stand in the barley crop (Fig. 4.7).

4.3.6 Rhizome Dry Weight

Eight weeks after seedling emergence, rhizomes were initiated in the pure stand of yarrow (Appendix 13, Plate 6). The increase in $\log_e$ rhizome weight (R_zW) with time was best explained by a linear model (Fig. 4.9); observed mean values are given in Appendix 10. The constant relative growth rate of R_zW (RGR_{Rz}) (Fig. 4.10) was responsible for the linear increase in weight. Rhizomes were present in the yarrow populations in association with the crops at 15 weeks after seedling emergence (Fig. 4.9). The R_zW of yarrow in the barley crop (0.01 g m^{-2}) was significantly less than when

▲ Pure stand of yarrow

$$\log_e SW = -8.131 + 2.48146t - 0.1769240t^2 + 0.004856680t^3$$

■ Yarrow in pea crop

$$\log_e SW = -12.231 + 4.29982t - 0.4667099t^2 + 0.016368209t^3$$

● Yarrow in barley crop

$$\log_e SW = -5.396 + 0.89868t - 0.0685582t^2 + 0.001920469t^3$$

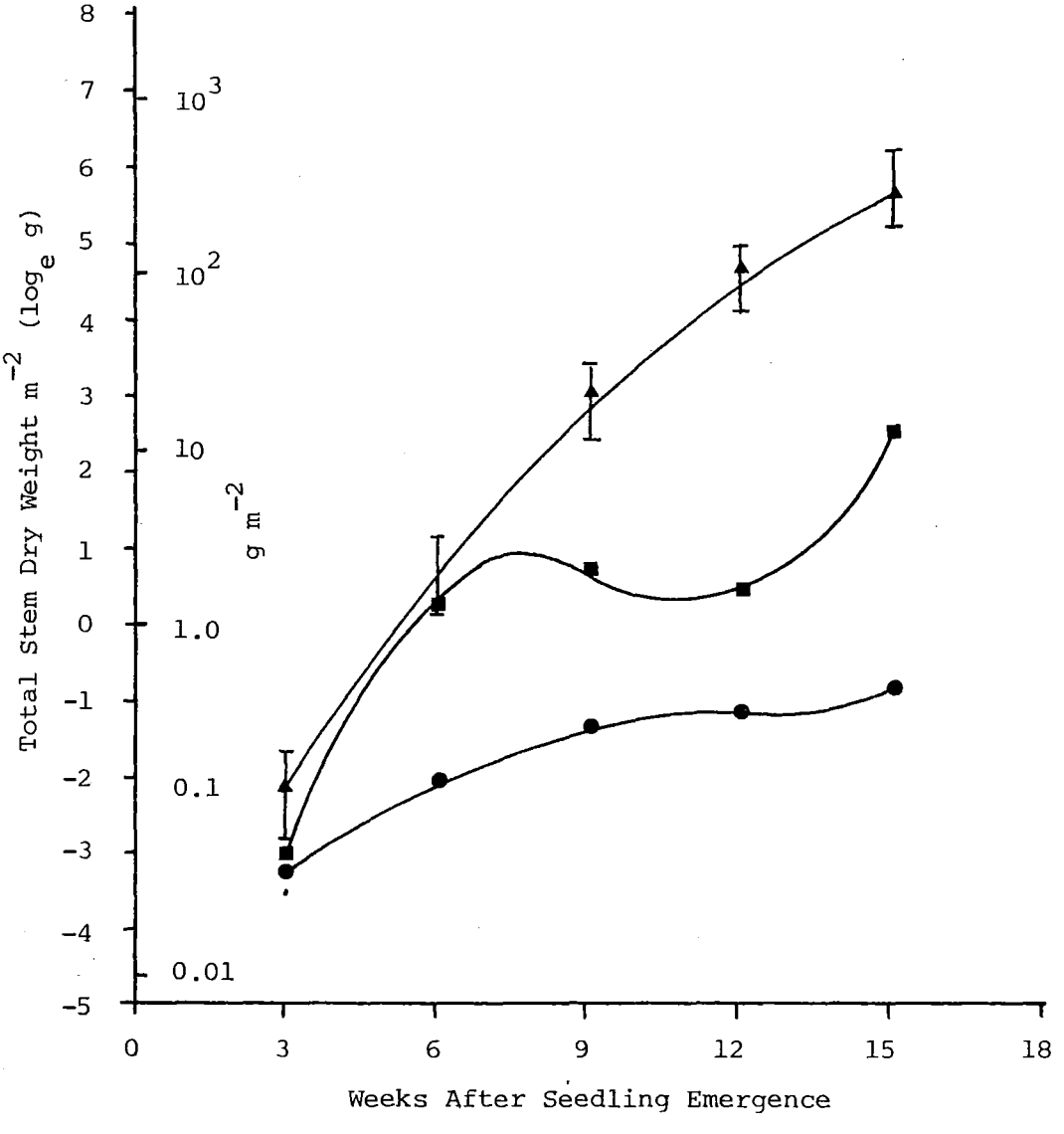


Figure 4.8: Progress curves of relative growth rate of stem dry weight, derived by differentiation of Figure 4.7. The bars are the confidence limits of the fitted values (95% probability); they apply equally to all curves.

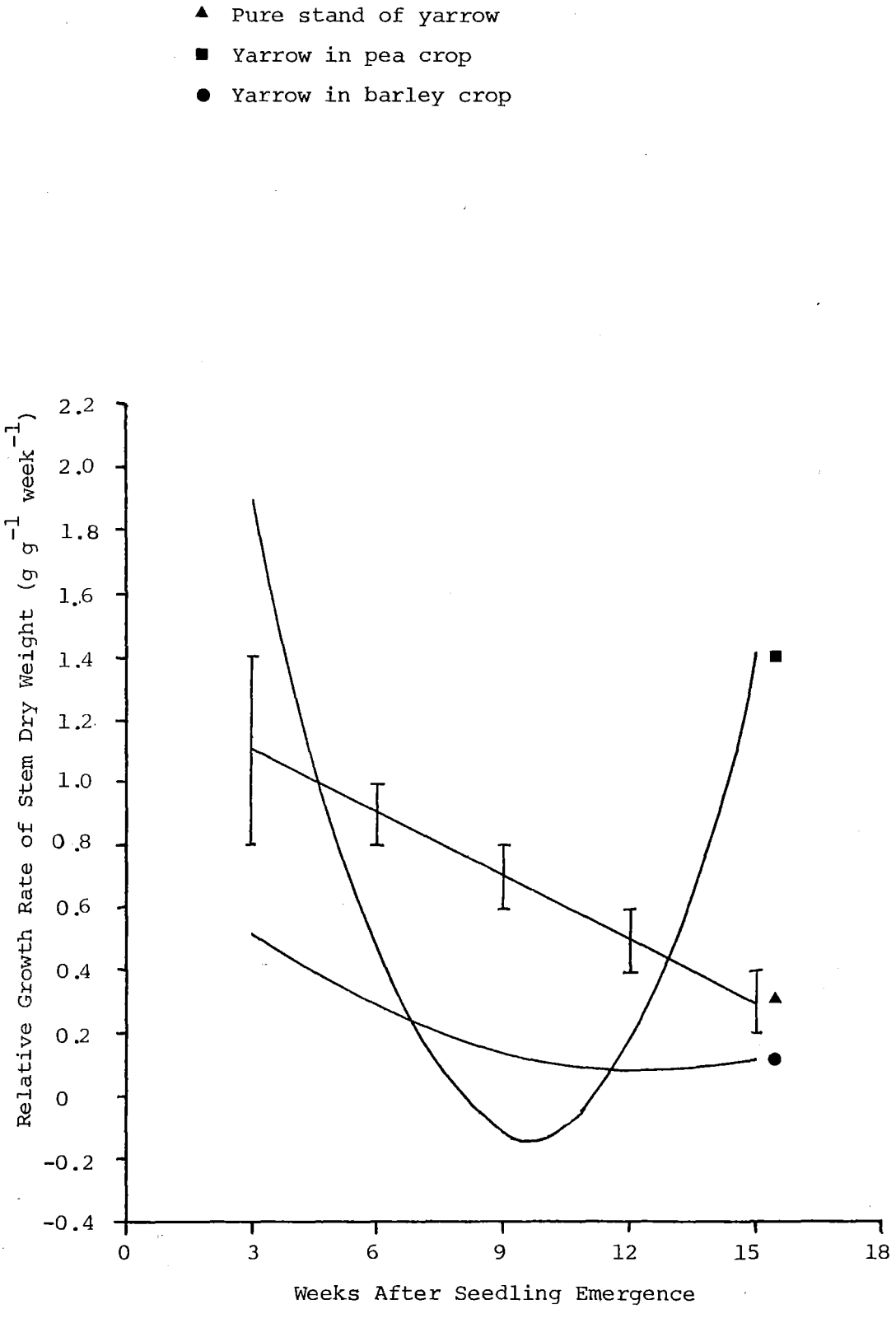

▲ Pure stand of yarrow
■ Yarrow in pea crop
● Yarrow in barley crop
Relative Growth Rate of Stem Dry Weight (g g-1 week-1)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
0
3
6
9
12
15
18
Weeks After Seedling Emergence

Figure 4.9: Progress curve of rhizome dry weight m^{-2}. The points are the observed means of the logarithms of total rhizome dry weight of seedling yarrow in pure stand and in association with the pea and barley crops; in the yarrow stands in the crops, rhizomes were present only at the final harvest. The line is the curve fitted to all individual samples in the pure stand of yarrow. The bars are the confidence limits for the fitted values (95% probability).

▲ Pure stand of yarrow

$\log_e R_z W = -2.876 + 0.45033t$

■ Yarrow in pea crop

● Yarrow in barley crop

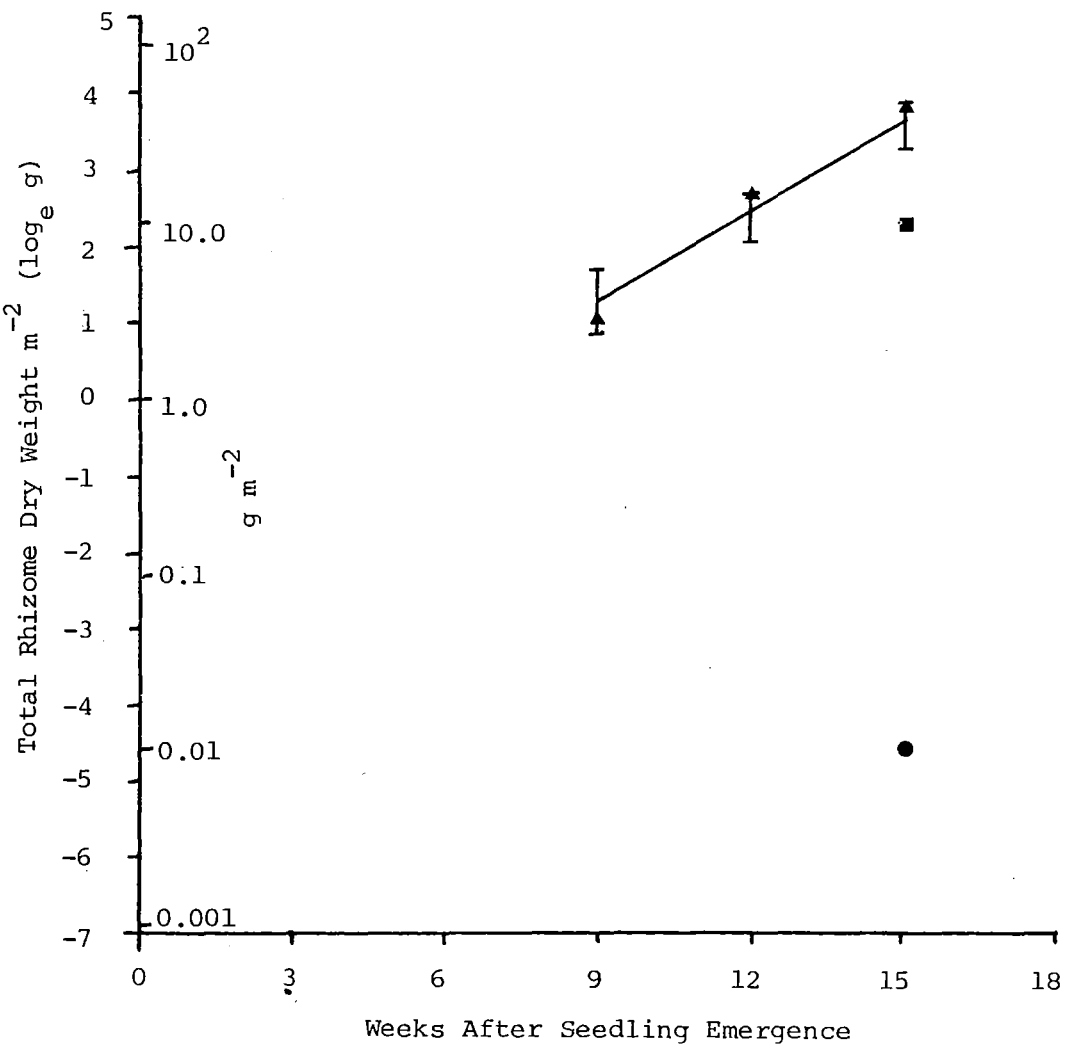
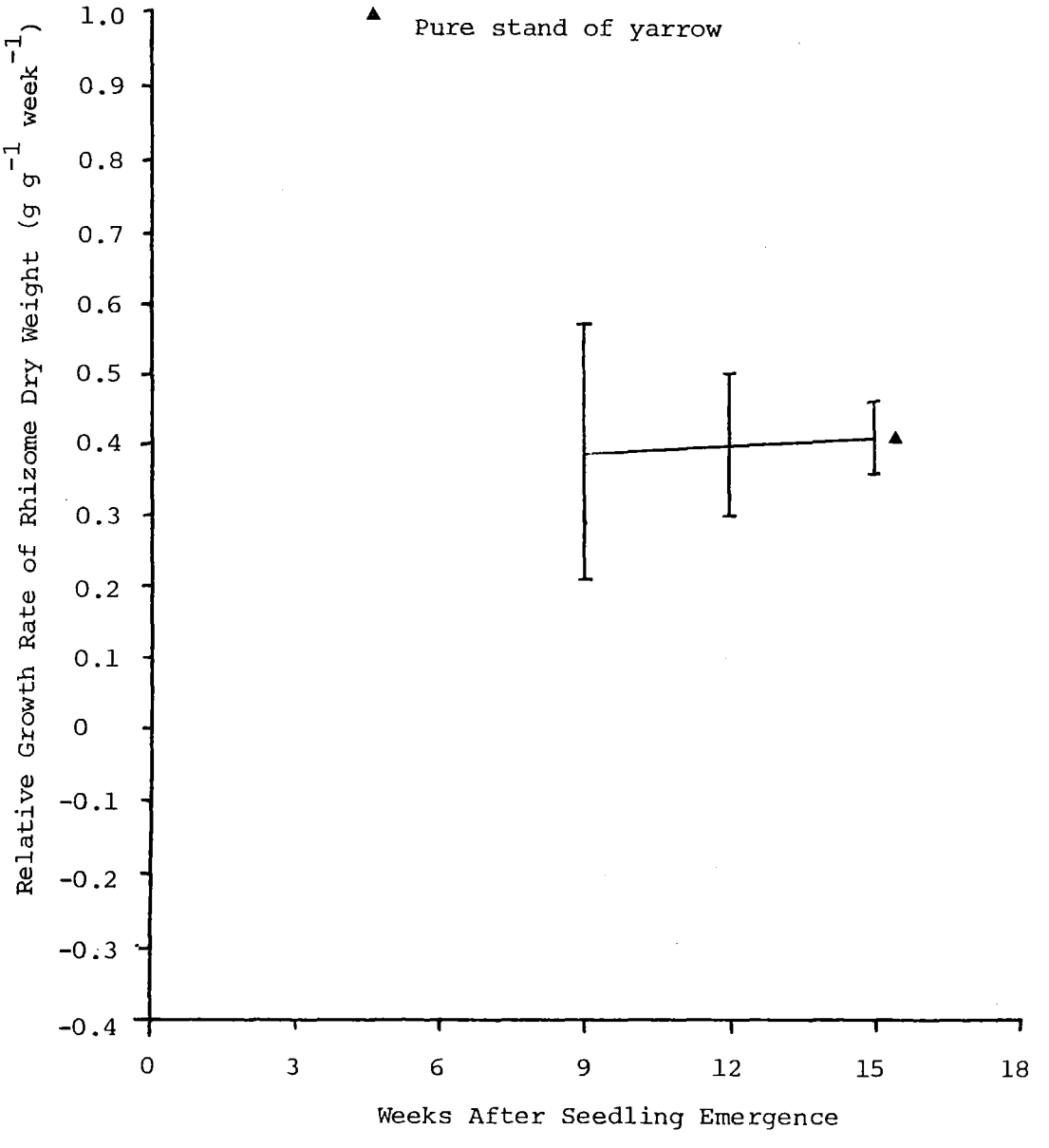


Figure 4.10: Progress curve of relative growth rate of rhizome dry weight, derived by differentiation of Figure 4.9. The bars are the confidence limits for the fitted values (95% probability).


Pure stand of yarrow
Relative Growth Rate of Rhizome Dry Weight (g g^{-1} week^{-1})
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0
3
6
9
12
15
18
Weeks After Seedling Emergence

yarrow was in association with the pea crop (10 g m^{-2}) and in pure stand (37 g m^{-2}); the latter two $R_z W$ values were also significantly different from each other.

4.3.7 Specific Leaf Area, Leaf Weight Ratio, and Leaf Area Ratio

The specific leaf areas (SLA) of all yarrow stands declined steeply from 3 to 7 weeks after seedling emergence (Fig. 4.11). Thereafter, while the SLA of the yarrow stand in the barley crop continued to increase, the SLA of the yarrow stands in association with the pea crops and in pure culture increased for 4 and 5 weeks respectively and then declined rapidly. The SLA of the yarrow stands in the crops were significantly greater than in the pure yarrow stand at 3 weeks after seedling emergence. At 6 weeks after seedling emergence, the SLA of the yarrow stand in the pea crop was significantly higher than in the yarrow stands in association with the barley crop and in pure culture. The above detailed difference in SLA between the yarrow stands in the pea crop and barley crop was also evident 3 weeks later; at 15 weeks after seedling emergence, the converse relationship was true.

The leaf weight ratio (LWR) of the yarrow stand in the pea crop generally increased with time (Fig. 4.12). However, the LWR of the yarrow stands in the barley crop and in pure culture increased up to 8 and 10 weeks after seedling emergence, respectively. Thereafter, the LWR of the yarrow in association with the barley declined for 4 weeks and then increased again while it continuously declined in the pure stand of yarrow. However, in spite of these differences in the trends of the LWR of the yarrow stands, they were not significantly different from each other.

The leaf area ratio (LAR) curves of the yarrow stands in the crops and in pure culture followed similar trends as detailed for the SLA (c.f. Figs 4.11 and 4.13). At 3 weeks after seedling emergence, the LAR of the yarrow stands in association with the crops were significantly greater than

Figure 4.11: Progress curves of specific leaf area, derived by subtracting the appropriate fitted $\log_e$ LW (Figure 4.5) form its fitted $\log_e$ LA (Figure 4.3). The bars are the confidence limits of the derived values (95% probability) and are presented to the left and right of the points on the curve to which they apply, in the case of yarrow populations in the barley crop and in pure stand, respectively; the confidence limits which apply to the points on the curve of the yarrow stand in the pea crop are presented on them.

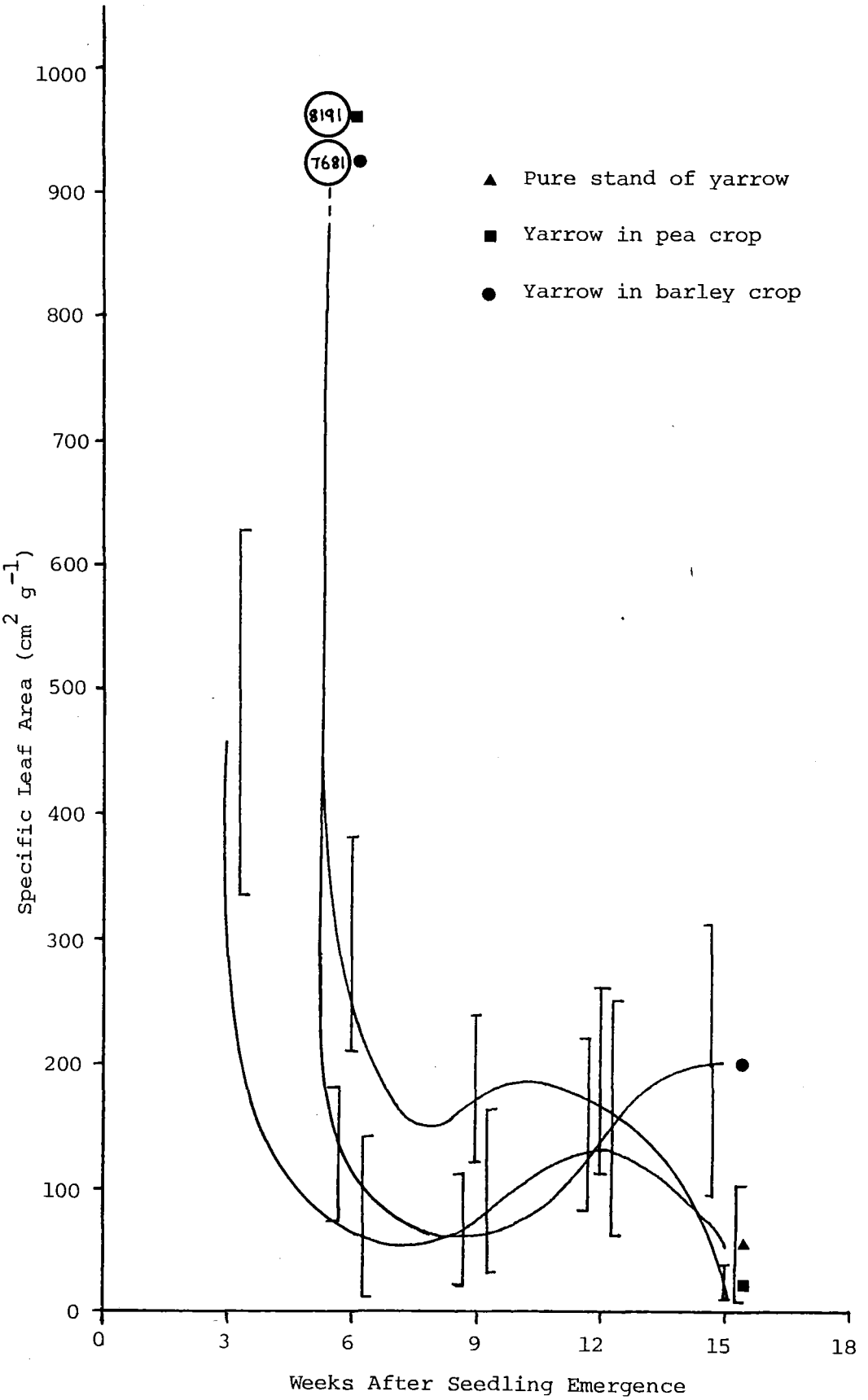

1000
900
800
700
600
500
400
300
200
100
0
Specific Leaf Area (cm^2 g^{-1})
8191
7681
▲ Pure stand of yarrow
■ Yarrow in pea crop
● Yarrow in barley crop
0
3
6
9
12
15
18
Weeks After Seedling Emergence

Figure 4.12: Progress curves of leaf weight ratio, derived by subtracting the appropriate fitted $\log_e$ W (Figure 4.1) from its fitted $\log_e$ LW (Figure 4.5). The bars are the confidence limits of the derived values (95% probability) and are presented to the left and right of the points on the curve to which they apply, in the case of yarrow populations in the barley crop and in pure stand, respectively; the confidence limits which apply to the points on the curve of the yarrow stand in the pea crop are presented on them.

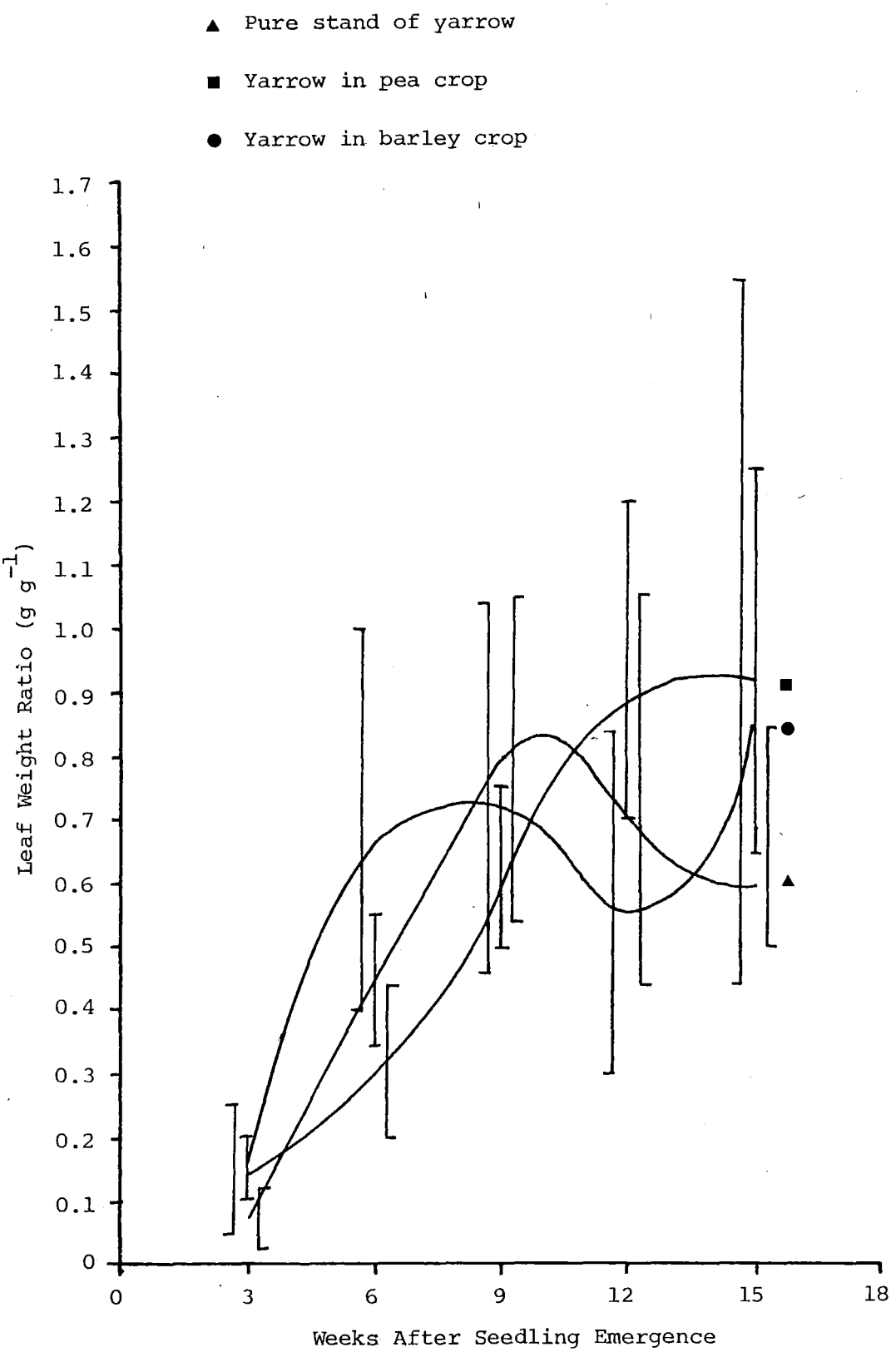
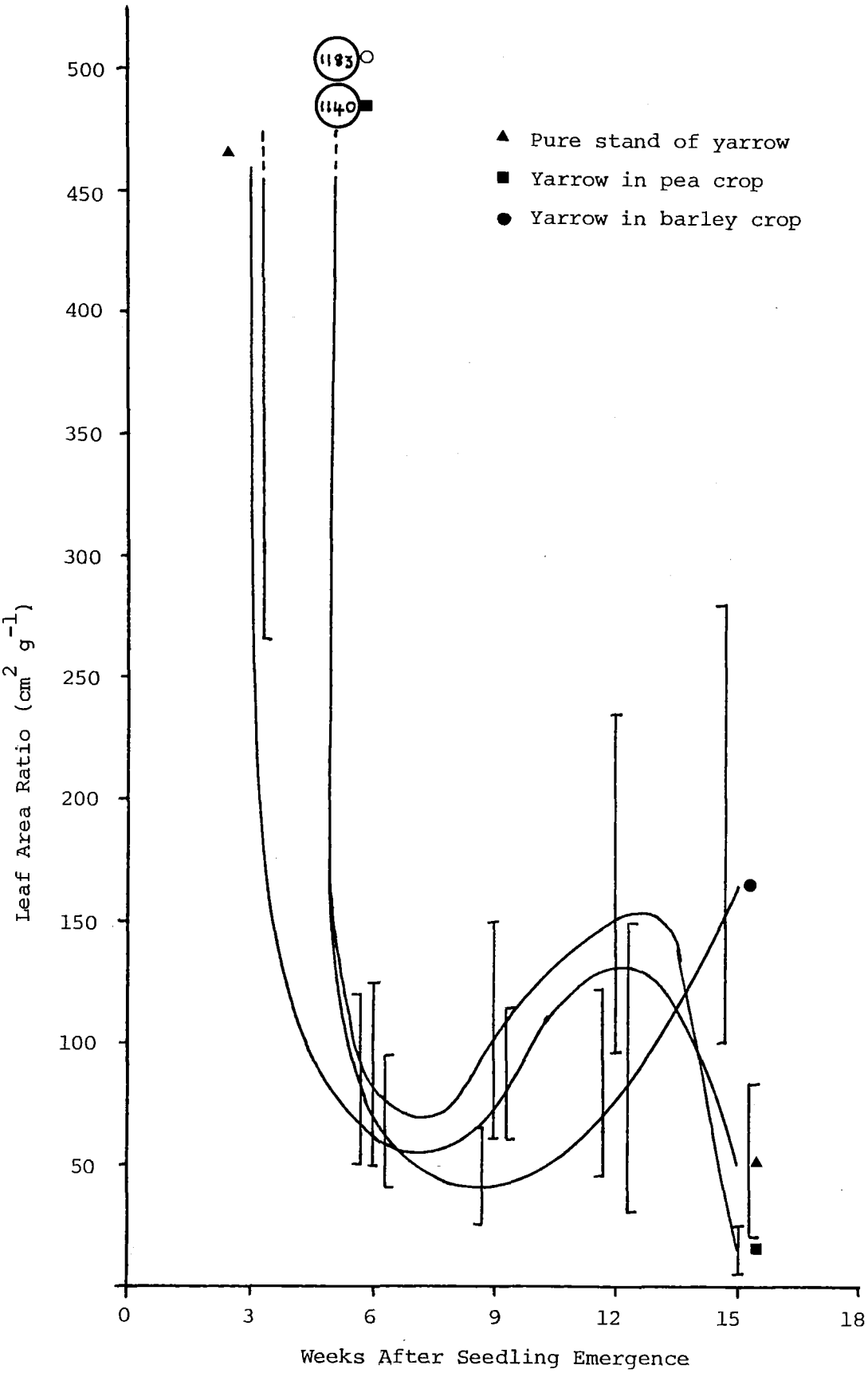

▲ Pure stand of yarrow
■ Yarrow in pea crop
● Yarrow in barley crop
Leaf Weight Ratio (g g⁻¹)
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
3
6
9
12
15
18
Weeks After Seedling Emergence

Figure 4.13: Progress curves of leaf area ratio, derived by subtracting the appropriate fitted $\log_e$ W (Figure 4.1) from its fitted $\log_e$ LA (Figure 4.3). The bars are the confidence limits of the derived values (95% probability) and are presented to the left and right of the points on the curve to which they apply, in the case of yarrow populations in the barley crop and in pure stand, respectively; the confidence limits which apply to the points on the curve of the yarrow stand in the pea crop are presented on them.


1183
1140
Pure stand of yarrow
Yarrow in pea crop
Yarrow in barley crop
Leaf Area Ratio (cm^2 g^{-1})
500
450
400
350
300
250
200
150
100
50
0
3
6
9
12
15
18
Weeks After Seedling Emergence

in the pure stand of yarrow. At 15 weeks after seedling emergence, the LAR of the yarrow in the barley crop was significantly greater than the other two yarrow stands.

4.3.8 Net Assimilation Rate

The net assimilation rates (NAR) of all three yarrow populations increased up to 6 weeks after seedling emergence (Fig. 4.14). Thereafter, while the NAR of the pure yarrow stand declined, the NAR of the yarrow in the crops declined for 4 to 5 weeks and increased again. From 3 to 9 and 6 to 9 weeks after seedling emergence, the pure stand of yarrow had a significantly higher NAR compared to that of the yarrow in the barley crop and pea crops, respectively. The NAR of the yarrow stand in the pea crop was significantly greater than in the yarrow in association with the barley crop at 3 and 15 weeks after seedling emergence.

4.3.9 Crop Yield

There was no significant difference between the grain yield of the barley crop growing in association with the yarrow population or as a pure stand (Table 4.3). However, the yarrow growing in association with the pea crop significantly reduced the machine dressed seed yield of the crop as compared to its yield in the pure stand.

4.3.10 Other Observations

By 13 weeks after seedling emergence, many yarrow plants in the pure stand had flower clusters at the centres of their leaf rosettes (Appendix 13, Plate 7). The yarrow in association with the crops did not flower.

Figure 4.14: Progress curves of net assimilation rate, derived by differentiation and division of the appropriate fitted curves of $\log_e$ W (Figure 4.1) and $\log_e$ LA (Figure 4.3). The bars are the confidence limits of the derived values (95% probability) and are presented to the left and right of the points on the curve to which they apply, in the case of yarrow populations in the barley crop and in pure stand, respectively; the confidence limits which apply to the points on the curve of the yarrow stand in the pea crops are presented on them.

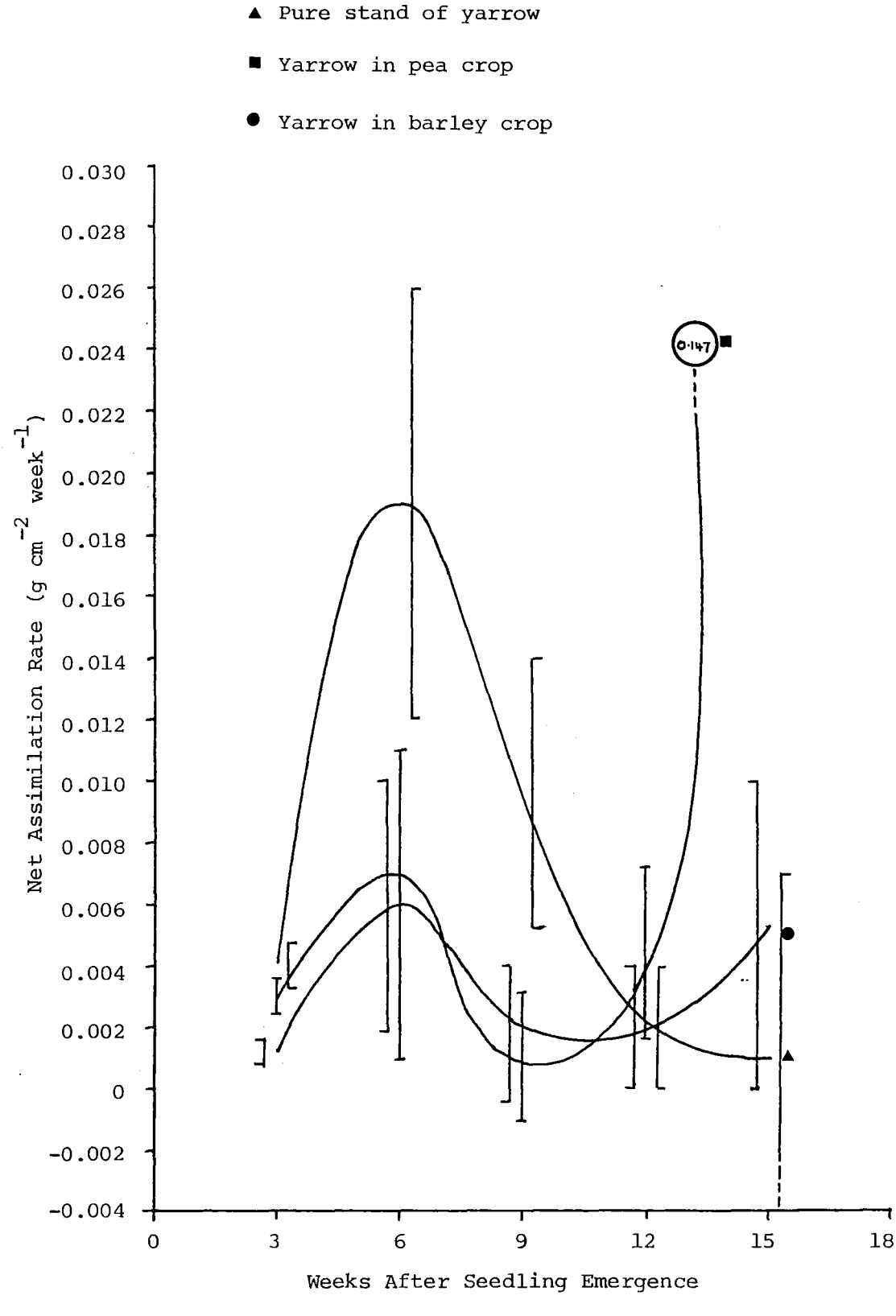

▲ Pure stand of yarrow
■ Yarrow in pea crop
● Yarrow in barley crop
0.030
0.028
0.026
0.024
0.022
0.020
0.018
0.016
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0
-0.002
-0.004
Net Assimilation Rate (g cm^{-2} week^{-1})
0.147
0
3
6
9
12
15
18
Weeks After Seedling Emergence

Table 4.3: Effect of seedling yarrow on the seed yield of barley and peas. (Each value is a mean of 6 replicates.)

Treatment	Mean Seed Yield* kg ha^{-1}
Barley	
- with yarrow	4723.65
- without yarrow	4876.65
L.S.D.$_{0.05}$	319.43
C.V. (%)	18.7
Peas	
- with yarrow	1698.11
- without yarrow	2327.01
L.S.D.$_{0.05}$	500.96
C.V. (%)	10.5

*Dried to constant weight at 30°C.

SECTION II: Yarrow after Crop Harvest

4.3.11 Total Dry Weight

The dead leaf fraction was included in this measurement. The changes in the $\log_e$ dry weight (W) of yarrow from 15 to 33 weeks after seedling emergence (i.e., up to 18 weeks after the crops were harvested) was adequately explained by a cubic model (Fig. 4.15); the observed means are given in Appendix 12. The changes in dry weights of the leaves, stems, and rhizomes (Appendix 12) of the three yarrow populations were reflected

Figure 4.15: Progress curves of the dry weight of yarrow m^{-2} after crop harvest and in the pure stand. The points are the observed means of the logarithms of the total dry weight. The lines are the curves fitted to all individual samples. The bars are the confidence limits for the derived values (95% probability); they apply equally to all the curves.

▲ Pure yarrow stand

$\log_e W = -22.454 + 3.85106t - 0.1573451t^2 + 0.0020321759t^3$

■ Yarrow after pea crop harvest

$\log_e W = -13.080 + 2.64517t - 0.1149879t^2 + 0.001589415t^3$

● Yarrow after barley crop harvest

$\log_e W = -40.640 + 5.458098t - 0.2192660t^2 + 0.002885417t^3$

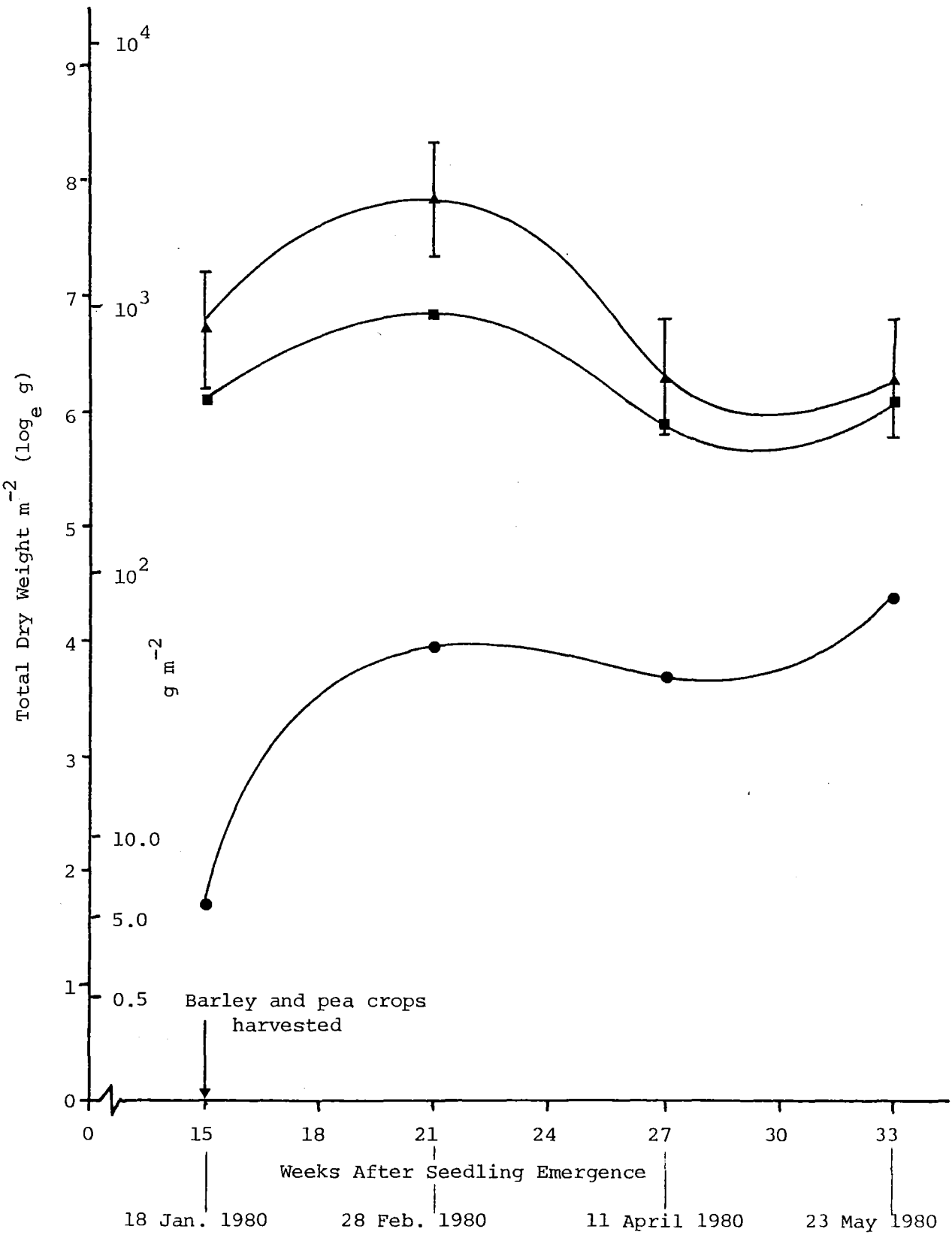
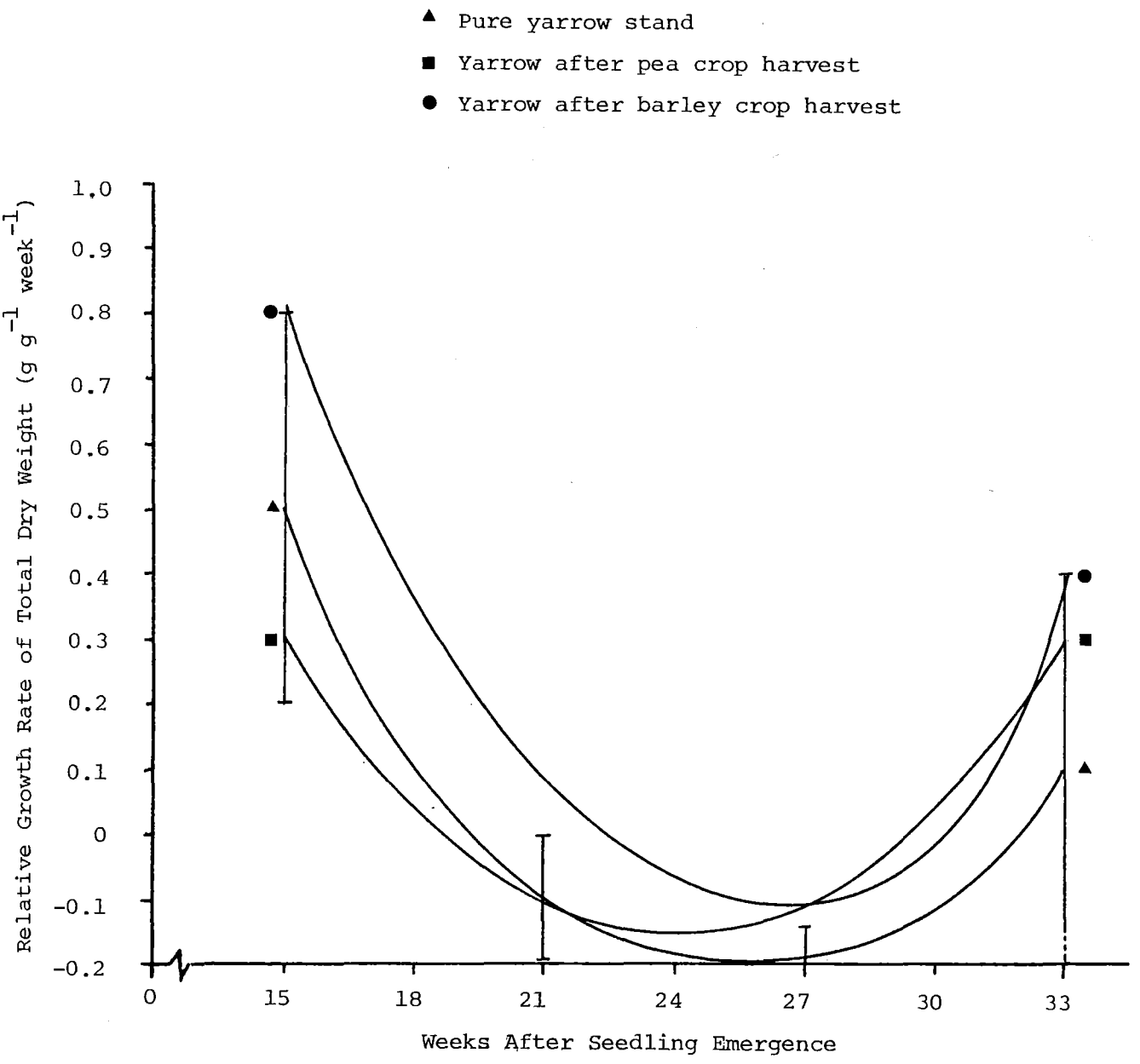


Figure 4.16: Progress curves of the relative growth rate of yarrow dry weight, derived by differentiation of Figure 4.15. The bars are the confidence limits of the fitted values (95% probability); they apply equally to all curves.


▲ Pure yarrow stand
■ Yarrow after pea crop harvest
● Yarrow after barley crop harvest
Relative Growth Rate of Total Dry Weight (g g-1 week-1)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
0
15
18
21
24
27
30
33
Weeks After Seedling Emergence

in the trends followed by W with time. The relative growth rates of the three yarrow populations were not significantly different from each other (Fig. 4.16). However, the initially higher W of the yarrow which was previously in association with the pea crop and in pure stand, compared to the yarrow population in the barley crop (i.e., at 15 weeks after seedling emergence), enabled them to maintain significantly greater W up to 33 weeks after seedling emergence (Fig. 4.15). The W of the three yarrow populations increased until the end of summer and then declined up to mid-autumn; they increased again in late autumn.

4.13.12 Total Rhizome Dry Weight

The change in $\log_e$ rhizome weights (R_zW) of the yarrow populations after barley and pea crops were harvested and in the pure yarrow stand during the same period was adequately explained by a cubic model (Fig. 4.17); the observed mean values are given in Appendix 12. The R_zW in all three yarrow stands increased from 15 to 23 weeks after seedling emergence (i.e., for 8 weeks after the crops were harvested); thereafter they decreased for the next 6 to 7 weeks, during the early part of autumn, before increasing again. The R_zW of the yarrow population which was previously in association with the barley crop was significantly less than in the other two yarrow stands throughout the growth period (Fig. 4.17). The relative growth rate of R_zW (RGR_{Rz}) of the yarrow population which was previously in association with the barley crop was significantly higher than in the other two yarrow populations at 15 weeks after seedling emergence (Fig. 4.18). However, its comparatively lower rhizome weight at 15 weeks after seedling emergence (Fig. 4.17) and the faster rate of decline of the RGR_{Rz} over the following 6 weeks (Fig. 4.18) did not allow its R_zW to increase to a similar level as that in the other populations (Fig. 4.17).

Figure 4.17: Progress curves of rhizome dry weight of yarrow m^{-2} in pure stand and after the crops were harvested. The points are the observed means of the logarithms of total rhizome dry weight. The lines are the curves fitted to all individual samples. The bars are the confidence limits for the derived values (95% probability); they apply equally to all the curves.

▲ Pure yarrow stand

$$\log_e R_z W = -41.251 + 5.77730t - 0.2289424t^2 + 0.002938966t^3$$

■ Yarrow after pea crop harvest

$$\log_e R_z W = -52.706 + 7.10621t - 0.2853521t^2 + 0.003746528t^3$$

● Yarrow after barley crop harvest

$$\log_e R_z W = -123.390 + 15.28508t - 0.6112257t^2 + 0.008010108t^3$$

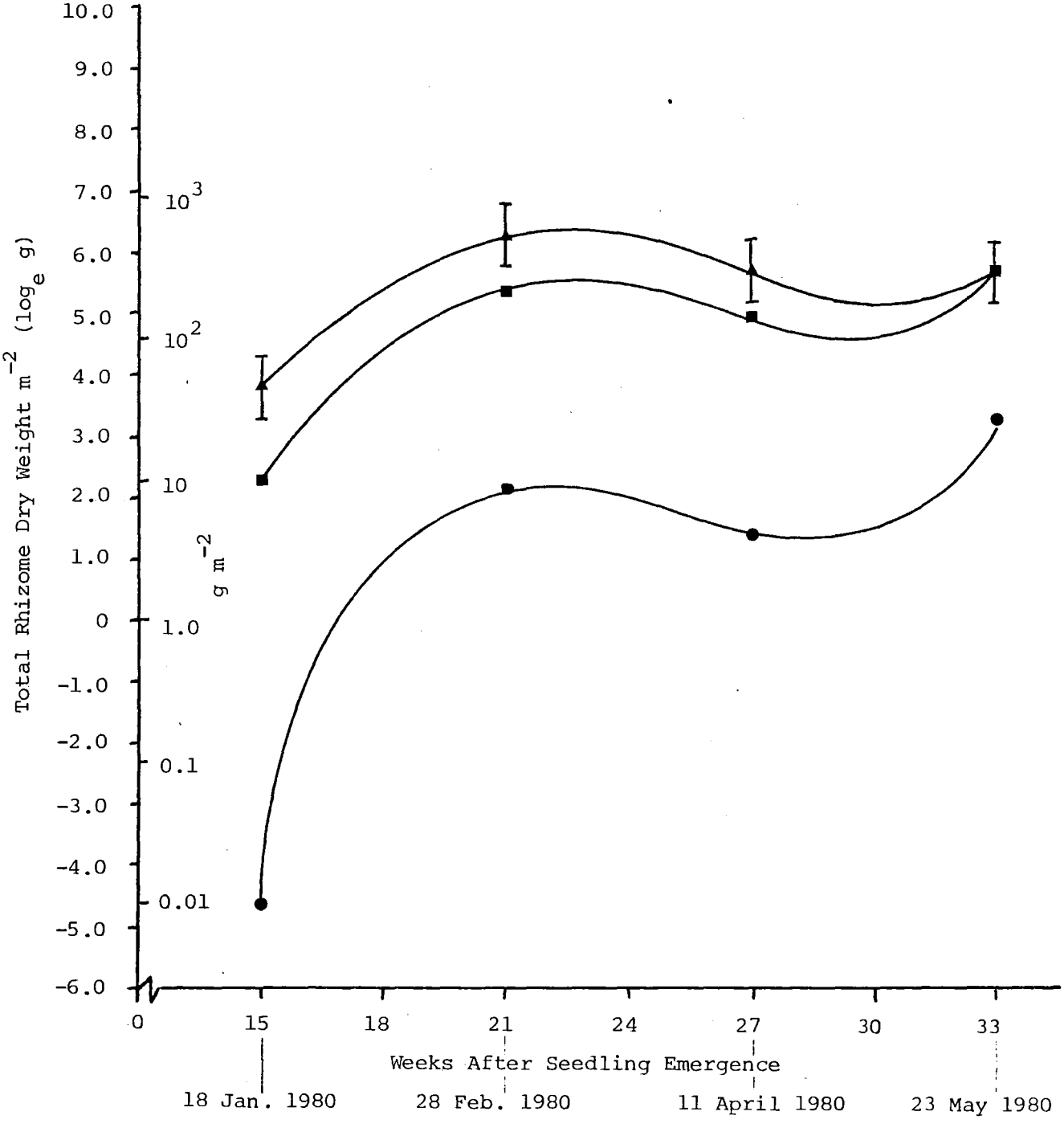
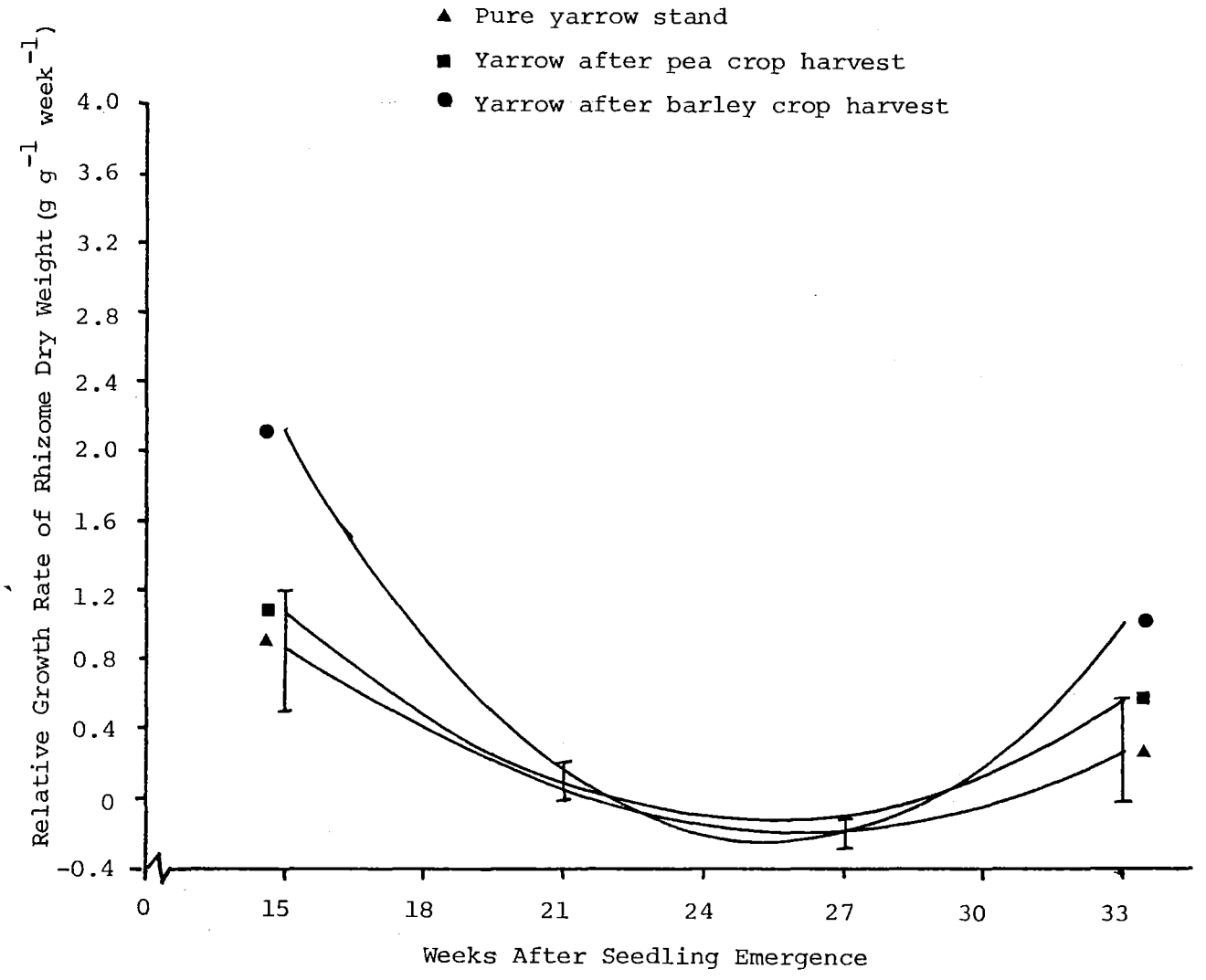


Figure 4.18: Progress curves of the relative growth rate of rhizome weight, derived by differentiation of Figure 4.17. The bars are the confidence limits of the fitted values (95% probability); they apply equally to all curves.


▲ Pure yarrow stand
■ Yarrow after pea crop harvest
● Yarrow after barley crop harvest
Relative Growth Rate of Rhizome Dry Weight (g g-1 week-1)
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
-0.4
0
15
18
21
24
27
30
33
Weeks After Seedling Emergence

4.4 DISCUSSION

When individuals of different species are released into a favourable environment, such as a cultivated field which is free of vegetation, initially their numbers increase rapidly (Harper and Gajic, 1961). However, this rate of increase does not continue indefinitely and as the established plants develop and grow, the intensity of interference between them increases. Harper (1961) stated that the time at which interference between plants starts is a function of their density. Therefore, depending on the plant numbers present, with time, the total population moves towards relative stability through process of mortality and plasticity (Harper and Gajic, 1961), with the population becoming self-regulatory within the framework of the powers of adaptability of individual species present. In an experiment where the weed *Agrostemma githago* was grown in pure stands and in association with wheat and sugar beet crops, Harper and Gajic (1961) observed that higher numbers of the weed established among the crops compared to its pure stand. It was suggested that at the initial stages of establishment, the presence of these crop plants provided a micro-environment which was more suitable for the germination and establishment of the *A. githago* seedlings.

In the present study, at 3 weeks after seedling emergence, there was a markedly higher number of yarrow seedlings in association with the barley crop, compared to their density in the pea crop and pure stand (Table 4.1). It is possible that the vigorously growing barley plants (Fig. 4.1) provided a more favourable environment for the germination of yarrow seeds and the emergence and establishment of their seedlings than did the comparatively slower growing pea plants or the open environment situation. However, with time, the density of yarrow plants growing with the crops and in pure stand stabilized and were not markedly different from each other by 9 weeks after seedling emergence (Table 4.1). In the early stages (i.e., up to 6 weeks after seedling emergence) the yarrow plants in association with the crops and in pure stand

were small, as indicated by their low total dry weight (Fig. 4.1) and were uniformly distributed in the field (Section 4.3.1). Therefore, it is unlikely that the loss of 52%, 34%, and 36% of the seedlings from the yarrow populations in association with barley and pea crops and their pure stands, respectively, from 3 to 6 weeks after emergence (Tables 4.1, 4.2) was associated with density-dependent self-thinning. The exact reason for this decline in density is not clear, though it is possible that some of the earlier emerging seedlings of yarrow may have been weakened by traces of the soil sterilant (methyl bromide + chloropicrin) remaining in the soil, leading to their subsequent mortality. However, the greater loss of yarrow seedlings from the population in association with the barley crop (from 3 to 6 weeks after seedling emergence), compared to the other two populations (Table 4.2), suggests that the presence of barley plants was detrimental to the yarrow plants. The nature of this detrimental effect was not studied, but is clearly different from the microclimate advantage offered by the barley that was discussed earlier. Overland (1966) reported that alkaloid substances present in barley plants are responsible for the poor germination and growth of *Stellaria media* in association with them. A similar allelopathic effect and/or the greater 'competitive' interference of barley plants with yarrow seedlings may have been responsible for the above observations.

Black (1958) found that when two cultivars of *Trifolium subterraneum* were grown in association, the larger seeded type with greater seed reserve produced a larger leaf area and was able to obtain a higher proportion of the available light; this enabled it to become the dominant cultivar. Similarly, Aspinall and Milthorpe (1959) and Aspinall (1960) showed that though barley (*Hordeum vulgare*) had a lower RGR than white persicaria (*Polygonum persicaria*), the larger seed size of barley gave rise to larger plants at emergence and this initial advantage led to the divergence in growth between the two species with time. This resulted in the growth of white persicaria becoming more and more suppressed. Other workers have stated that the success of one species

over the other, when they are growing in association, depends on their relative times of emergence, relative seedling size at emergence, and subsequent RGR (Milthorpe, 1961) and the variations in their growth habit (Trenbath, 1976).

Yarrow seeds are very small, 0.16 mg seed^{-1} (Appendix 6), compared to those of barley (87 mg seed^{-1}) and peas (240 mg seed^{-1}). Owing to the comparatively small mass of seed reserve, the yarrow seedlings at emergence were much smaller than those of the crops. The yarrow seedlings also had a more or less prostrate vegetative growth habit (Appendix 13, Plate 7) compared to the more erect growing crop plants. Therefore, although yarrow and crop seedlings emerged at the same time (Section 4.3.1), and the RGR_W of the yarrow in association with the barley and pea crops were 1.1 and 2.3 g g^{-1} week^{-1} compared with 1.0 and 0.8 g g^{-1} week^{-1} of the crops, respectively, at 3 weeks after seedling emergence (Fig. 4.2), the relatively smaller seedling size and growth habit of yarrow led to a rapidly established initial divergence in the dry weight of the yarrow populations and the associated crops (Fig. 4.1).

When different species of plants grow in close proximity to one another, they have been found to 'competitively' interfere with each other for the limited resources of light, water, and nutrients (Donald, 1963). Apart from or in addition to 'competitive' interference, various forms of 'non-competitive' interference, including allelopathic effects (Overland, 1966; Rice, 1979) or the presence of certain species, promoting disease incidence in another species (Chamblee, 1958; Sandfaer, 1970) or the promotion of lodging of one species by another (Probst, 1957) have been reported to occur. Both kinds of interference lead to the suppression of growth and development of plants (Trenbath, 1976).

Since there was no observable disease incidence or the possibility of lodging of yarrow plants growing in association with the barley and pea crops, 'competitive' interference for light or water or mineral nutrients or

any combination of them and/or the allelopathic effects of the crop plants on yarrow may have been responsible for the delayed rhizome initiation (Section 4.3.6), total suppression of flowering (Section 4.3.10) and the retardation of vegetative growth of yarrow (Fig. 4.1).

With the growth of the barley and pea crops, their LA increased up to 6 and 9 weeks after seedling emergence, respectively (Fig. 4.3). Being relatively taller plants than the yarrow, their increasing LA intercepted an increasingly higher proportion of the incident light and the photosynthetically active radiation (PAR) available to the yarrow populations present beneath the crop canopies decreased (Appendix 7). This interference for light between the yarrow and the crops may be an important factor responsible for the above detailed suppression of the growth and development of yarrow stands in association with the crops. However, throughout the growth and development of the crops there was a substantially greater light availability to the yarrow stand in association with the pea crop than with the barley crop (Appendix 7). The markedly lower LA of the pea crop, compared to the barley, up to 6 weeks after seedling emergence (Fig. 4.3); the greater length of time the pea crop required to attain its maximum LA; the lower maximum LA of the pea crop compared to the barley crop; and the differences in the leaf architecture and orientation of the leaves in the two crops, no doubt contributed to the observed differences in light transmission. Even at the time of crop harvest, the yarrow population in association with the barley crop received only 21% of the total available PAR compared to 84% received by the stand in the pea crop (Appendix 7). At this time, the greater PAR availability to the yarrow stand in the pea crop was partly associated with the shedding of the dead leaves by the pea crop, which allowed greater penetration of light to the yarrow stand. In contrast, the dead leaves of the barley crop remained on the plants and may have acted as a barrier to light penetration to the yarrow stand beneath it. The greater availability of light to the yarrow stand in the pea crop may have been an

important reason for its markedly better growth and development, compared to the yarrow population in the barley crop (Fig. 4.1).

During the period of crop growth and development, the amount of rainfall, which was the only source of replenishment of the soil water, decreased while the air temperature increased (Appendix 1). The rising temperature may have led to the faster rate of growth of the crops and this in turn would have resulted in an increased depletion of soil water by these plants. Therefore, it is possible that interference for water between the crop plants and yarrow growing with them would have occurred. This may have been an additional factor responsible for the observed retardation in the growth and development of yarrow plants (Fig. 4.1). The present study did not allow the separate assessment of whether interference occurred between the crops and yarrow stands for mineral nutrients and/or whether other forms of 'non-competitive' interference, including allelopathy, were present. However, it is possible that the rapidly growing crops would have obtained a greater share of the limited supply of soil nutrients. The presence of root nodules on the pea plants (Section 4.2.6) would have enabled them to fix atmospheric nitrogen. Thus, the yarrow plants in association with the pea plants, may have had a relatively greater supply of soil nitrogen available to them than when they were growing with the barley plants, leading to improved growth and development of yarrow in association with the pea crop (Fig. 4.1). Overland (1966) found that allelopathic substances produced by the barley plants played an important role in suppressing the growth of *Stellaria media*. There is no published evidence to suggest that pea plants are capable of exerting similar 'non-competitive' interference effects on other species. Therefore, it is not unreasonable to suggest that the allelopathic effects of the barley plants on yarrow may have contributed to the greater suppression of the growth and development of the latter species.

Interference between yarrow and the respective crop stands resulted in a retardation of the development of LA (Fig. 4.3) and the growth of LW (Fig. 4.5), SW (Fig. 4.7) and R_ZW (Fig. 4.9) of yarrow. Owing to the large errors involved in recovering the yarrow roots from the soil and subsequently separating them from the crop roots, it was not possible to assess the effect of interference on root growth and development. However, other studies have shown that the reduced availability of light alone suppressed the growth of yarrow roots (Bourdôt, 1980; Table 3.4). Since interference for light (Appendix 7) and other factors, discussed earlier, occurred between yarrow and the two crops, it would have undoubtedly suppressed the growth of the yarrow roots. Reduction in the growth and development of the root systems of plants has been found to affect their ability to utilize the available water and mineral nutrients and this in turn resulted in the reduced growth and development of their shoot systems (Harper, 1977). The effects of interference on the differential growth and development of the root and shoot systems of plants are closely inter-related, but were not determined in the present experiment.

The suppression of the LA of the yarrow populations in association with the crops (Fig. 4.3) resulted from the marked reduction in their RGR_A compared to the values in the pure stand of yarrow, up to 9 weeks after seedling emergence (Fig. 4.4). Even though the RGR_A of the yarrow stands in the crops increased substantially during the latter stages of crop growth and development, the initial retardation continued to be evident even at the time of crop harvest with the LA of yarrow in the barley and pea crops being 0.08 $m^2\ m^{-2}$ and 0.6 $m^2\ m^{-2}$, respectively, compared to 5.42 $m^2\ m^{-2}$ of the pure stand of yarrow (Fig. 4.3). Although both crops suppressed the development of LA in the yarrow stands in association with them, the suppressive effect by the pea crop was markedly less than by the barley crop (Fig. 4.3). This was due to the significantly higher RGR_A of the yarrow in the pea crop, up to 6 weeks after seedling emergence, compared to the RGR_A of the yarrow

associated with the barley crop (Fig. 4.4). The higher availability of PAR to the yarrow stand in the pea crop compared to when yarrow was in association with the barley crop (Appendix 7) would have undoubtedly been, at least partially, responsible for the above detailed difference in RGR_A between the yarrow stands in association with the crops; the differences in interference for other factors, discussed earlier, may have also contributed. Owing to the difference between the RGR_A of the two yarrow stands in the crops, an initial divergence was established in their respective LA (Fig. 4.3) and this was maintained through time, even though after 12 weeks from seedling emergence the RGR_A of the yarrow in the barley crop was higher than in the yarrow stand in association with the pea crop (Fig. 4.4). The relatively higher RGR_A of the yarrow in the barley crop compared to when it was in association with the pea crop, after 12 weeks from emergence, was certainly not due to higher PAR availability (Appendix 7). The lesser interference for soil factors between yarrow and the barley crop compared to between yarrow and the pea crop may have been responsible for the differences in their RGR_A during the latter stages of crop growth. The RGR_A of the yarrow in the barley and pea crops increased rapidly from 6 and 9 weeks after seedling emergence, respectively (Fig. 4.4). This period of increase in RGR_A coincided with the decline in the LA of the respective crops (Figs 4.3 and 4.4) and appears to be closely related to the amount of PAR available to the yarrow stands (Appendix 7). As a result of increasing light availability, the photosynthetic rate of plants usually increases (Black, Chen and Brown, 1969). The above detailed changes in RGR_A and LA of the yarrow stands in association with the different crops may have resulted from the increased availability of photosynthetic material as a consequence of increased PAR availability.

The RGR_{LW} (Fig. 4.6) and RGR_{SW} (Fig. 4.8) and the resulting LW and SW (Figs 4.5, 4.7), of the yarrow stands in association with the crops and in pure stand followed similar trends to their respective RGR_A and LA

(Figs. 4.3, 4.4). The close relationship between the amount of PAR available to the different yarrow stands and their likely photosynthetic output may be responsible for the observed similarities in trends of the relative growth rates of LA, LW, and SW and the resulting total weights.

Plant growth and development is affected by environmental factors, such as light, water, mineral nutrients, oxygen, and carbon dioxide (Donald, 1963; Trenbath, 1976) and physiological factors, including translocation, transpiration and partitioning of metabolites for new tissue synthesis and storage (Black, Chen and Brown, 1969). However, the primary determinant of growth and development of plants can be considered to be the amount of effective photosynthetic material they produce. Leaves are the most important photosynthetic organs, and light interception and photosynthetic rate depend to a large extent, upon the leafiness (LAR) and efficiency of the leaves (NAR) of the plants (Causton and Venus, 1981). Interference among plants can lead to changes in their LAR and NAR, and as a result affect their rates of carbon assimilation. For example, Aspinall (1960) found that when white persicaria (*Polygonum lapathifolium*) and barley (*Hordeum vulgare*) plants were grown together, the LAR of white persicaria was increased, while its NAR decreased, compared to values obtained in a pure stand. However, the increasing LAR was unable to adequately compensate for the declining NAR; this would have undoubtedly resulted in a reduction in the quantity of assimilate available to the white persicaria plants growing in association with the barley plants. The reduced availability of assimilates would have been responsible for the suppression of RGR_W which in turn resulted in reduction in the growth (W) of white persicaria, compared to its pure stand.

When yarrow was growing with the crops, its LAR, at 3 weeks after seedling emergence, was markedly higher than in the pure stand of yarrow (Fig. 4.13). This is a typical response to shading (Hughes, 1965; Bourdôt, 1980). As there were no marked differences in the proportion of the total

assimilate retained by the leaves (LWR) of yarrow stands in the crops and in pure stand (Fig. 4.12), the higher leafiness of the yarrow stands in the crops was associated with their thinner and more expanded leaves, as measured by a higher SLA (Fig. 4.11). At the same time, there was no marked difference between the NAR of the yarrow in the pea crop and in the pure stand (Fig. 4.14). This, plus the increase in LAR, resulted in the relatively higher RGR_W of the yarrow in the pea crop compared to the pure stand of yarrow (Fig. 4.2). However, the W of the yarrow in the pea crop and in pure stand, at 3 weeks after emergence, were similar (Fig. 4.1). This would have resulted from the RGR_W of the pure stand of yarrow being greater than that of the yarrow in the pea crop at some stage prior to 3 weeks after seedling emergence. In the yarrow stand associated with the barley crop, at 3 weeks after seedling emergence, the effect of the decreased NAR was greater than the increase in LAR and this resulted in the RGR_W being more suppressed compared to the yarrow growing with peas and yarrow in the pure stand. However, the W of the yarrow in the barley crop was not markedly different from the other two stands of yarrow, at 3 weeks after seedling emergence (Fig. 4.1). The reason for this is similar to that discussed above in relation to RGR_W and W of the yarrow in the pea crop and in pure stand.

From 3 to 9 weeks after seedling emergence, the LAR of all three yarrow stands declined rapidly (Fig. 4.13) while the NAR of the yarrow in the crops were markedly suppressed, compared to the pure stand of yarrow (Fig. 4.14). This led to the reduction in the RGR_W of the yarrow growing in association with the crops (Fig. 4.2), resulting in their markedly lower W compared to the pure stand of yarrow. However, as the SLA (Fig. 4.11) and NAR (Fig. 4.14) of the yarrow in the pea crop was relatively less retarded than when the yarrow was in association with the barley crop, the RGR_W of the former stand of the yarrow remained comparatively higher than in the latter yarrow population, up to about 7 weeks after seedling emergence

(Fig. 4.2). In the latter stages of crop growth and development, the increase in RGR_W of the yarrow in the barley crop (Fig. 4.2) resulted from the increase in its LAR and NAR (Figs 4.13, 4.14). The rapid increase in NAR (Fig. 4.14) more than compensated for the decline in the LAR (Fig. 4.13) in the yarrow in association with the pea crop, from 12 to 15 weeks after seedling emergence, and this resulted in its increased RGR_W (Fig. 4.2). However, as the rapid increase in NAR in the yarrow population in association with the pea crop was markedly greater than the combined increase in LAR and NAR in the yarrow stand in the barley crop, from 12 to 15 weeks after seedling emergence, the RGR_W of the former population of yarrow increased relatively more rapidly than in the latter population (Fig. 4.2); the rapidity of increase in RGR_W of the yarrow in association with the pea crop enabled it to reach a W which was not markedly different from that of the pure stand of yarrow, by 15 weeks after seedling emergence (Fig. 4.1). As the amounts of PAR available to the different yarrow stands were closely related to their trends in LAR and/or NAR (Appendix 7; Figs 4.13 and 4.14), which in turn was related to their RGR_W (Fig. 4,2), shading appears to be an important factor responsible for the markedly different growth of the three yarrow populations (Fig. 4.1). Differences in interference for water and mineral nutrients and possibly the allelopathic effects of barley may have also been responsible for the differences in W of the three yarrow stands. However, as interference affected LAR and/or NAR, there is no doubt that the differences in the amount of photosynthetic assimilate available to the yarrow stands led to their observed growth trends.

Studies on the effect of crop interference on the reproduction of weed populations are limited. Aspinall and Milthorpe (1959) found that as the LA and root growth of barley plants declined with the onset of flowering, white persicaria growing in association with the crop, flowered and produced abundant seed. The ability of the white persicaria to flower in the latter stages of crop growth and development appears to be due to the reduced

interference for light and soil factors between the two species. In the present study, though reductions in interference for light (Appendix 7) and possibly for soil factors occurred in the period after flowering of the crops (i.e., 10 weeks after seedling emergence), sexual reproduction was totally suppressed in the yarrow populations in association with the barley and pea crops (Section 4.3.10). Earlier work showed that 23.7% of total available PAR was sufficient to initiate flowering in individually growing seedling yarrow plants (Table 3.1). However, although the yarrow population in the pea crop received more than 23.7% PAR up to 15 weeks after seedling emergence (Appendix 7), they failed to flower, while the yarrow population in pure stand initiated flowering at 13 weeks after seedling emergence (Appendix 13). Therefore, it appears that in the presence of adequate light, other types of interference between the yarrow and pea plants and possibly intra-specific interference between yarrow plants themselves prevented flowering. In the yarrow stand in association with the barley crop, the low PAR availability from 6 to 9 weeks after seedling emergence (Appendix 7), as well as other types of interference discussed above, may have prevented flowering. In addition to the total absence of flowering, rhizome initiation was also delayed by 5 to 6 weeks in the yarrow stands in association with the crops (Fig. 4.9; Appendix 13, Plate 6). However, the $R_z W$ of the yarrow in the pea crop was 10 g m^{-2} compared to 0.01 g m^{-2} when in association with the barley crop (Fig. 4.9). The higher PAR availability to the yarrow stand in the pea crop (Appendix 7) may have been an important factor responsible for the improved growth of rhizomes.

The final grain yield of the barley crop was not suppressed by the yarrow growing in association with it (Table 4.3). There is no doubt that this was associated with the marked retardation of yarrow growth by the barley crop (Fig. 4.1). However, the comparatively better growth of yarrow in the pea crop led to a substantial reduction in the pea seed yield (Table 4.3). Since W of the pea crops in pure stand and in association with the yarrow

were not different from each other up to 12 weeks after seedling emergence (Fig. 4.1), it is not unreasonable to suggest that the decline in pea seed yield was not due to the suppression of the early vegetative growth of the crop. The reason for the decline in pea seed yield is not clear, and since the main objective of the present study was to assess the effects of the crops on the growth and development of seedling yarrow, the effects of yarrow on crop performance was not investigated in depth. However, as flowering in the pea plants occurred at approximately 10 weeks after seedling emergence, it is likely that early interference from yarrow may have suppressed flower primordia initiation as well as retarded the growth and development of the flower primordia that were initiated. Apart from or in addition to the above detailed effects on the sexual reproduction of pea plants, interference may also lead to the decrease in the rate of flowering, reduce the number of flowers formed at each node, increase flower abortion, shorten the duration of the flowering period, and also adversely affect other yield components, such as the number of pods per plant, seeds per pod, and seed weight. Detrimental effects on any of the above components or on a combination of them would undoubtedly lead to a reduction in the final pea seed yield.

In the first 6 weeks after the crops were harvested, the W of the yarrow stands which were in association with them increased rapidly (Fig. 4.15); there was a 2 and 8 fold increase in W of the yarrow stands which were in the pea and barley crops, respectively. Maximum temperature of over 20^{o}C and increased rainfall (Appendix 1), together with the increased PAR availability after crop removal and lack of other types of interspecific interference, discussed above, would have contributed to the increased growth of the yarrow stands during this period. The increase in R_zW (Fig. 4.17) was the single most important factor contributing to the increase in W, although increases in LW and SW also occurred (Appendix 12); the R_zW of the yarrow stand from the barley crop increased from 0.1 g m^{-2} to 9.0 g m^{-2} in the 6 weeks period immed-

iately following crop harvest, while in the yarrow stand from the pea crop it increased from 10 g m^{-2} to 221 g m^{-2} during the same period. Although the RGR_{R_zW} of the yarrow stand from the barley crop was higher than in the yarrow stand from the pea crop (Fig. 4.18), the markedly higher R_zW of the latter stand at crop harvest (Fig. 4.17), compared to the former yarrow stand, was responsible for the continued differences in R_zW of the two yarrow stands during this period. A similar explanation can be presented for the markedly higher W of the yarrow stand from the pea crop compared to the yarrow from the barley crop (Figs 4.15, 4.16); at the end of 6 weeks after crop harvest, the W of the yarrow from the pea crop was 944 g m^{-2} compared to 52 g m^{-2} of the yarrow population previously associated with the barley crop.

The W of the two yarrow stands previously associated with the crops declined from 6 to 13 weeks after crop harvest (Fig. 4.15) and this was mainly due to the death of the older leaves which was reflected in the decline in LA and LW (Appendix 12); R_zW also declined during this period (Fig. 4.17). The reduction in solar radiation and the lower temperatures during this period (Appendix 1) may have been responsible for the loss of the older and larger leaves of yarrow stands from the crops; smaller and thicker leaves were formed during this period (autumn) in these yarrow stands (Appendix 13) and is clearly an adaptation to the coming winter. The reason for the decline in R_zW from 6 to 13 weeks after crop harvest is not clear, although the reduced availability of photosynthetic material, due to the respective decrease in light availability (Appendix 1) and LA (Appendix 12), may have led to the death of newly-formed rhizomes.

In late autumn (13 to 18 weeks after crop harvest), the W of the yarrow stand which were previously associated with the crops increased (Fig. 4.15) due to the increase in their RGR_W (Fig. 4.16). Similar to the period of increase in W for the first 6 weeks after crop harvest, the rapid increase in R_zW (Fig. 4.17) was mainly responsible for the increase in W during the

late autumn period; the stem and leaf fractions showed very slow growth (Appendix 12). A lack of substantial growth of the aerial parts of the yarrow stands from the crops may have enabled most of the photosynthetic material available at this time to be utilized for rhizome growth and development. A high rate of rhizome growth in late autumn was also observed by Bourdôt (1980).

The W, LA, LW, SW, and $R_z W$ of the pure stand of yarrow followed similar trends as detailed for the yarrow stands from the crops, during the 18 weeks period from 15 weeks after seedling emergence (Figs 4.15, 4.16, 4.17, 4.18; Appendix 12).

The present study clearly indicated that the barley crop was superior to the pea crop in suppressing the growth and development of seedling yarrow. The higher initial seedling vigour, quicker attainment of maximum LA, higher maximum LA, more efficient shading of the yarrow plants and possibly the higher interference for water and mineral nutrient and the possible allelopathic effects of barley on yarrow, enabled barley to suppress the growth and development of seedling yarrow better than the pea crop. It is suggested that other crops, particularly other cereals, with similar growth characteristics to barley, may be equally efficient in suppressing seedling yarrow infestations on arable land. The rapid growth of the surviving yarrow seedlings after crop harvest indicates the need to destroy these seedlings immediately after the crops have been removed from the field. A delay of 6 weeks in destroying the surviving yarrow seedlings could lead to a substantial increase in rhizome bud reserves and greatly complicate the management of yarrow on arable land.

CHAPTER 5

THE NATURE OF INTERFERENCE BETWEEN SEEDLING YARROW AND BARLEY OR PEA PLANTS AND THE AGGRESSIVITY OF YARROW

5.1 INTRODUCTION

Higher plants are known to hinder or promote the growth and development of one another when they grow as neighbours. The hinderance of the activity of one plant by another, whether of the same species or of a different species, may occur owing to competitive interference between them for limited soil and aerial resources (e.g., water, mineral nutrients, and light); and/or by non-competitive interference such as by the release of toxic substances to the environment (allelopathy) or modifying the environment and thus providing for the prevalence of pests and diseases (Harper, 1964). In other instances, a plant species may promote the growth and development of an associated species by providing nutrients of limited supply (e.g., legumes supply nitrogen to non-leguminous plants, (De Wit, Tow and Ennik, 1966; Hall, 1974b)), by protecting it from predators (Harper and Sagar, 1953) and other pests and diseases (Harper, 1964), or by modifying the environment to such an extent that it is more favourable for the germination, establishment and growth and development of other species (e.g., conditions may become increasingly conducive for 'shade-tolerant' plants).

In a field situation, where diversity of species is the rule and monoculture the exception, both the density and proportion of species present vary in space and time. In 'additive' experimental designs used to study the behaviour of two species growing together, both the effects of density and relative proportions of the species are confounded and it is not possible to separate the intensity of their independent effects. De Wit (1960) used

a 'substitution' design which was able to overcome the above detailed problems of the 'additive' design. In this technique, species 'A' and 'B' were grown in varying proportions (i.e., 0A:100B, 25A:75B; 50A:50B; 75A:25B; and 100A:0B) while maintaining the overall density constant. Harper (1977) stated that in most plant populations, changes in the proportions of species over time is invariably accompanied by changes in their densities and thus De Wit's technique does not truely represent what occurs in the field. However, the use of substitution designs in field and pot experiments has the distinct advantage of removing the requirement for special and artificial methods of separating root and shoot systems, as in other techniques (e.g., Donald, 1958; Snaydon, 1979). Because the technique enables the study of the effects of relative density of comparable species upon the interactions between them, many workers have used it in studies on plant interference (e.g., De Wit, 1965; Van den Bergh and Elberse, 1970; Hall, 1974b).

In De Wit's technique, the substitution (or replacement) of one species by another species is complicated by the fact that the effect of a single plant of one species may not be equivalent to that of another. It is usually assumed that the effects of a single plant of each species is equivalent at the optimum plant density for that species growing in monoculture. On this basis, the equivalent density for a species is calculated. For example, if (a) the optimum density of species 'A' in monoculture is 10 plants m^{-2} and (b) the optimum density of species 'B' in monoculture is 30 plants m^{-2}, then 1 plant of 'A' is considered to be equivalent to 3 plants of 'B'. This method of using optimum density to determine plant equivalence may not be very accurate. However, in the absence of a better technique, it is commonly used in studies of interaction between crop species (Martin and Snaydon, 1982). When interactions between a weed species and a crop are studied, the above detailed method of determining plant equivalence is no longer applicable as there is no such thing as an optimum density of a pure

stand of weeds. In such instances, many workers have assumed a 1:1 plant equivalence ratio (e.g., Schreiber, 1967; Ivens and Mlowe, 1980).

In the above detailed 'Replacement Series' studies, the relative yield total (RYT) has been used by many workers as an agronomic assessment of the productivity of mixtures of plant species (e.g., Trenbath, 1974; Fisher, 1979). The RYT is the sum of the fractions of the yields of plant components, relative to their monoculture yields, based on a per plant basis:

$$RYT = 0.5 \left[\frac{Y_{ij}}{Y_{ii}} + \frac{Y_{ji}}{Y_{jj}} \right]$$ (McGilchrist and Trenbath, 1971)

where Y_{ij} = yield plant^{-1} of species 'i' grown with species 'j'

Y_{ji} = yield plant^{-1} of species 'j' grown with species 'i'

Y_{ii} = yield plant^{-1} of species 'i' in monoculture

Y_{jj} = yield plant^{-1} of species 'j' in monoculture.

However, Hall (1974a, b) found it suitable and convenient to represent the relative yields (r) of species 'a' and 'b' on a per stand basis:

relative yield of species 'a' (r_a) = $\frac{O_{ab}}{M_a}$

relative yield of species 'b' (r_b) = $\frac{O_{ba}}{M_b}$

where O_{ab} = the yield of species 'a' in mixture with species 'b'

O_{ba} = the yield of species 'b' in mixture with species 'a'

M_a = yield of species 'a' in monoculture

M_b = yield of species 'b' in monoculture.

He calculated RYT by summing up r_a and r_b. The RYT is more useful as an ecological assessment of mixtures than an agronomic assessment (Martin, personal communication).

De Wit (1960) suggested that:

(a) if the RYT was significantly greater than 1, then the component species were not in full competitive interference and were, at least partially, utilizing different environmental resources,

(b) when RYT = 1, the species were either in complete interference ('perfect competition') or mutually exclusive of one another and using identical resources or were not interfering with each other, and

(c) when the RYT was significantly less than 1, both competitive and non-competitive processes were in operation. These interpretations of RYT are now generally accepted (Trenbath, 1974).

In the quantitative studies of plant interference by De Wit and Van den Bergh (1965), De Wit, Tow and Ennik (1966) the observed effects were interpreted as 'competition for space' and interference for different growth factors and resources. De Wit (1960) stated that the subdivision of this complex process " ... is not necessary, always inaccurate, and is therefore inadvisable". However, Hall (1974a) pointed out that if the principal factor(s) for which interference occurred could be identified, the argument of whether or not interactions occur among the factors becomes irrelevant. He extended De Wit's analysis to identify interference between species for mineral nutrients (Hall, 1974a, b). Up to the present time, this technique has not been used to study the interference for light and water (i.e., the 'replacement series' method). This may be owing to the greater difficulties involved in assessing these factors.

The 'replacement series' type of experiment is also useful in evaluating the 'competitive ability' of the plant species at different relative densities. McGilchrist (1965) suggested a method for determining 'competitive ability' based on the arithmetic increase or decrease in yield

of one species when grown in mixture, compared with its yield in pure stand and the increase or decrease in yield of the other species similarly calculated. Later, McGilchrist and Trenbath (1971) modified the above method to measure the proportional changes in yield. They termed this measure 'Aggressivity' (A). For example, the aggressivity of species 'a' in relation to species 'b' is measured by:

$$A_{ab} = 0.5 \left[\frac{Y_{ab}}{Y_{aa}} - \frac{Y_{ba}}{Y_{bb}} \right]$$

where Y_{ab} = yield plant^{-1} of species 'a' grown in mixture with species 'b',

Y_{aa} = yield plant^{-1} of species 'a' in pure stand,

Y_{ba} = yield plant^{-1} of species 'b' grown in mixture with species 'a',

and Y_{bb} = yield plant^{-1} of species 'b' in pure stand.

If $A_{ab} = 0$ species 'a' relative to species 'b' is equally 'competitive'; if the yield of species 'a' is 30% greater when grown with species 'b' than in pure stand and the yield of species 'b' is similarly decreased, then the aggressivity of species 'a' is 0.3 and conversely that of species 'b' is -0.3. In this instance, species 'a' is the aggressor and species 'b' is suppressed. This method of evaluating the aggressivity has been used by many workers (e.g., Remison and Snaydon, 1980; Martin and Snaydon, 1982).

Another technique that has been used in recent studies of plant interactions was developed from the method used by Donald (1958) to study interference for aerial and soil factors separately or when both occur simultaneously. This allowed for the assessment of the relative importance of interference for 'above ground' and 'below ground' factors and the identification of possible interactions between them. Donald's technique involved the growing of two plant species, in pots which had vertical soil and aerial

partitions placed perpendicular to one another, so that there were four possible conditions: no interaction between them or either their roots or shoots or both were able to intermix. Other workers used similar techniques to study the nature of interference between plant species (e.g., Aspinall, 1960; Lambert, 1967; King, 1971; Barrett and Campbell, 1974). However, there were major drawbacks to these techniques. Firstly, the amount of aerial space and soil volume available to the plants were different in treatments: secondly, the overall densities between the treatments varied. Other modifications of Donald's technique had some treatments with partitions and others without them (e.g., Rhodes, 1968 ; Eagles, 1972). However, their presence or absence, especially the aerial partitions, can modify the micro-environment of the plants (Warren and Lill, 1975) and markedly vary their growth (Rennie, 1974).

Snaydon (1979) improved on the technique used by Schreiber (1967), who in turn had modified Donald's technique, by eliminating the drawbacks detailed above. In this technique and those by Schreiber (1967), Rhodes (1968) and Eagles (1972), it was possible to vary the overall density and stand size and the root and shoot densities could also be varied independently. However, unlike similar studies, Snaydon's method enabled the varying of the relative density of the interacting species, while still retaining the ability to study their root and shoot interactions separately. This enabled De Wit's (1960) analysis of 'crowding for the same space' to be studied in greater detail by separating the total interaction into interference for 'root space' and 'shoot space'.

There are some limitations in Snaydon's technique for evaluating plant interactions. Firstly, the aerial partitions shade and reduce plant growth (Rennie, 1974; Warren and Lill, 1975); the use of reflective materials and the orientation of the partitions in north-south (N-S) direction minimizes this effect (Snaydon, 1979). Secondly, the interactions between plants is limited to one lateral dimension (Schreiber, 1967; Eagles,

1972; Snaydon, 1979). Thirdly, the aerial partitions can act as wind shelters or wind channels, depending on the direction of the wind, and the soil partitions restrict normal root development. All these can modify the growth and development of the plants and thus vary the nature of interactions between them compared to that occurring in a field situation. Rennie (1974) and Snaydon (1979) state that the effects of these limitations are not great. Even though there are limitations, many workers have continued to use Snaydon's technique (e.g., Remison and Snaydon, 1980; Martin and Snaydon, 1982) owing to the lack of a better method.

In the present study, Snaydon's technique was used to evaluate the mechanisms of interference between seedling yarrow and barley or pea plants. The effects of the relative density of the species upon the interactions between them were studied by applying the 'Replacement Series' technique (De Wit, 1960). The nature of root interference was further investigated by chemical analysis of the shoot material to establish whether or not there was competitive interference for the mineral nutrients N, P, and K.

5.2 EXPERIMENTAL RESULTS

Experiment 1

Evaluation of the effects of root and/or shoot interference from barley (*Hordeum vulgare* cv. Zephyr) plants on the growth and development of seedling yarrow.

5.2.1 Materials and Methods

5.2.1.1 Layout and Experimental Design

Specially designed wooden boxes (0.9 x 0.9 x 0.3 m) were lined with horticultural grade polythene and drainage holes were made at the bottom. Each box was divided into self-contained compartments, 0.15 m wide, using galvanised iron sheets, both above and below ground. The aerial partitions

were in the 0.9 x 0.15 m strips; this enabled the height of the above-ground partitions to be adjusted gradually as the plants increased in height. These partitions were lined with 'Mylar' reflector foil to ensure good distribution of light to the plants growing between them. The partitions and the rows of yarrow and barley plants were arranged in four different ways (Fig. 5.1), so as to create: (a) no interaction, (b) root interaction only, (c) shoot interaction only, and (d) both root and shoot interaction, between the species.

The Wakanui silt loam soil used in the experiment had 32 parts/10^6, nitrogen (N), 18 parts/10^6 phosphorus (P), 15 parts/10^6 potassium (K); the pH was 6.7 On 1 November 1980, N, P, and K were added to the shredded soil at the rate of 357 kg ha^{-1} ammonium sulphate (75 kg ha^{-1} N), 250 kg ha^{-1} Flomaster super phosphate (20 kg ha^{-1} P), and 125 kg ha^{-1} potassium sulphate (50 kg ha^{-1} K), respectively, and mixed thoroughly. This soil was filled into the boxes and lightly compacted. The soil surface in each box was flush with its upper edge. The soil was sterilized in a similar way to that detailed in Chapter 4, using methyl bromide gas and allowed to ventil-late for 7 days. The boxes were appropriately arranged (Fig. 5,1) in the field, with the aerial partitions in a north-south direction to minimise shading, in a randomized block design. Each treatment (i.e., a, b, c and d in Fig. 5.1) was replicated 4 times. There were sufficient number of boxes to carry out 4 sequential harvests of each treatment.

5.2.1.2 Seed Material

Sun dried seed heads were collected in May 1980 and seed cleaning was done as detailed in Chapter 2. The cleaned seed was stored at room temperature in a polythene bag until used in the experiment. Barley seed was obtained from a commercial source.

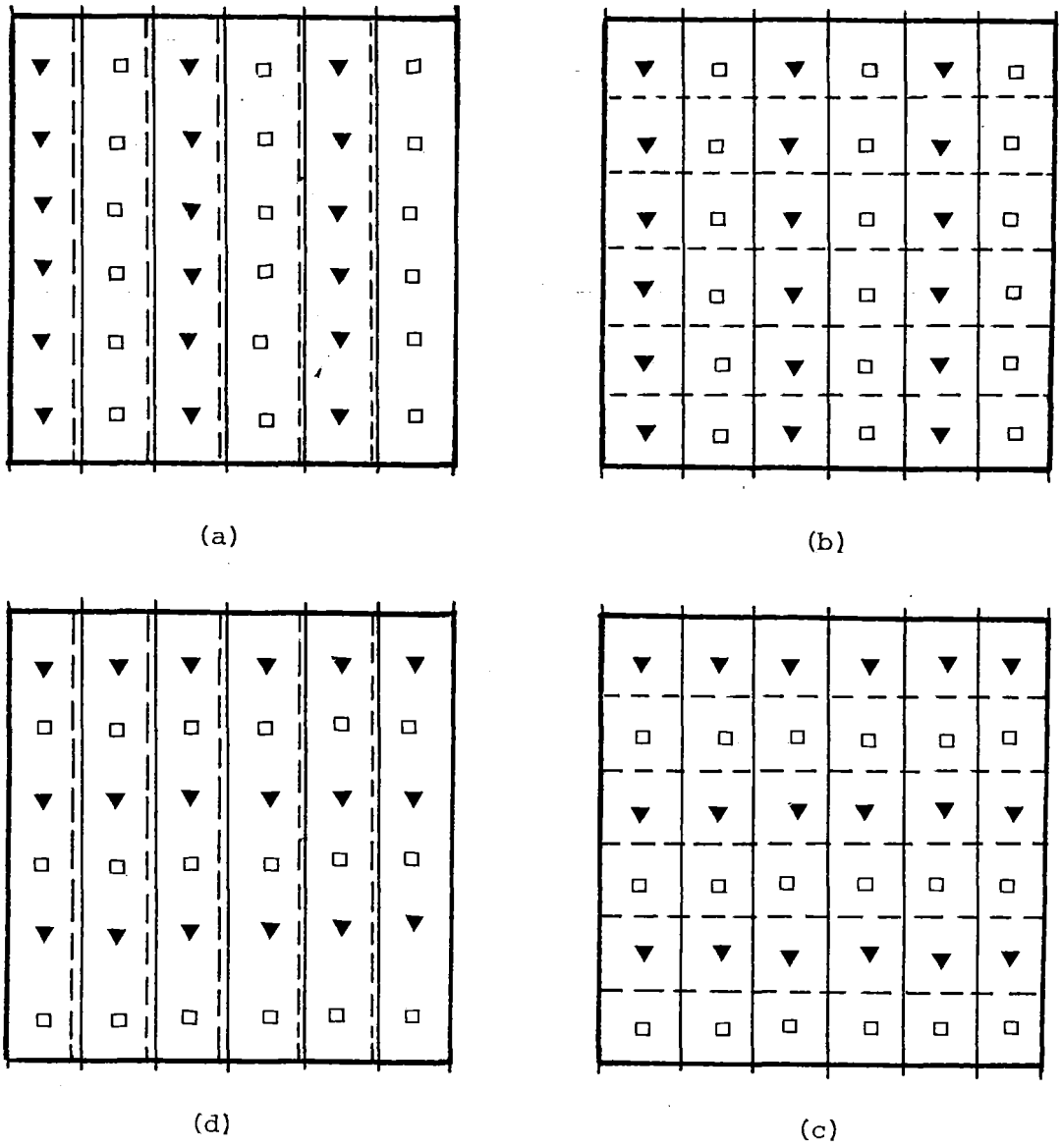


Figure 5.1: Planting arrangements of yarrow (▼) and barley or pea (□) plants (Experiments 1 and 2, respectively) to give (a) no interference, (b) root interference only, (c) shoot interference only, and (d) both root and shoot interference, between the species. Aerial partitions (full lines) arranged in a north-south direction. The soil partitions (dashed lines) are slightly displaced for clarity.

5.2.1.3 Establishment and Management

On 15 November 1980, pregerminated yarrow and barley seed were planted in rows as indicated in Figure 5.1. Adjacent rows were spaced 15 cm apart, while the within-row spacing of plants was 5 cm. The yarrow seeds were placed on the soil surface and covered with a thin layer of soil while the barley seeds were planted 1 cm deep.

Seedlings of yarrow and barley emerged from the soil on 20 November 1980. One week after emergence, the first set of aerial partitions were placed and their height was adjusted, by placing additional partitions, as the plants increased in height. All treatments were irrigated to maintain the soil close to field capacity throughout the experiment.

5.2.1.4 Sampling Procedure and Measurements

Each treatment was harvested at 21, 35, 49, and 63 days after seedling emergence. At each harvest, the soil was carefully washed from the roots of the plants. From the second harvest onwards, it was not possible to distinguish and satisfactorily dis-entangle the roots of the two species in the treatments (b) and (d) (Fig. 5.1). Therefore, this data was omitted from the evaluation of the performance of yarrow growing with the barley plants. Since a previous study had shown that seedling yarrow did not affect the vegetative growth of barley (Chapter 4), measurements were carried out only on the yarrow seedlings. The shoots of the yarrow plants were fractionated into leaves and stems. The leaf area of each sample was measured using a Licor area meter. All plant fractions, including the rhizome fraction at the final harvest, were oven dried to a constant weight at 80^{o}C. In the first 3 harvests, total dry weight included the leaf and stem weights only; in the final

harvest, total dry weight also included its rhizome weight.

5.2.1.5 Statistical Analysis

Analyses of variance of leaf area, the weights of leaves, stems and rhizomes, and total weight, were carried out using the 'Genstat' statistical package.

5.2.2 Results

5.2.2.1 Total Dry Weight

The changes in dry matter accumulation in the leaf, stem, and rhizome fractions of yarrow plants in the presence of root, shoot or full interference were reflected in the total weight of yarrow. Root interference suppressed the growth of yarrow before shoot interference had any effect (Fig. 5.2a). Compared to the growth of yarrow in the absence of interference between the species, root interference suppressed its growth significantly more than when only shoot interference occurred. The decline in the growth of yarrow in the presence of full interference was less than the additive effects when each type of interference occurred independently.

5.2.2.2 Total Leaf Area

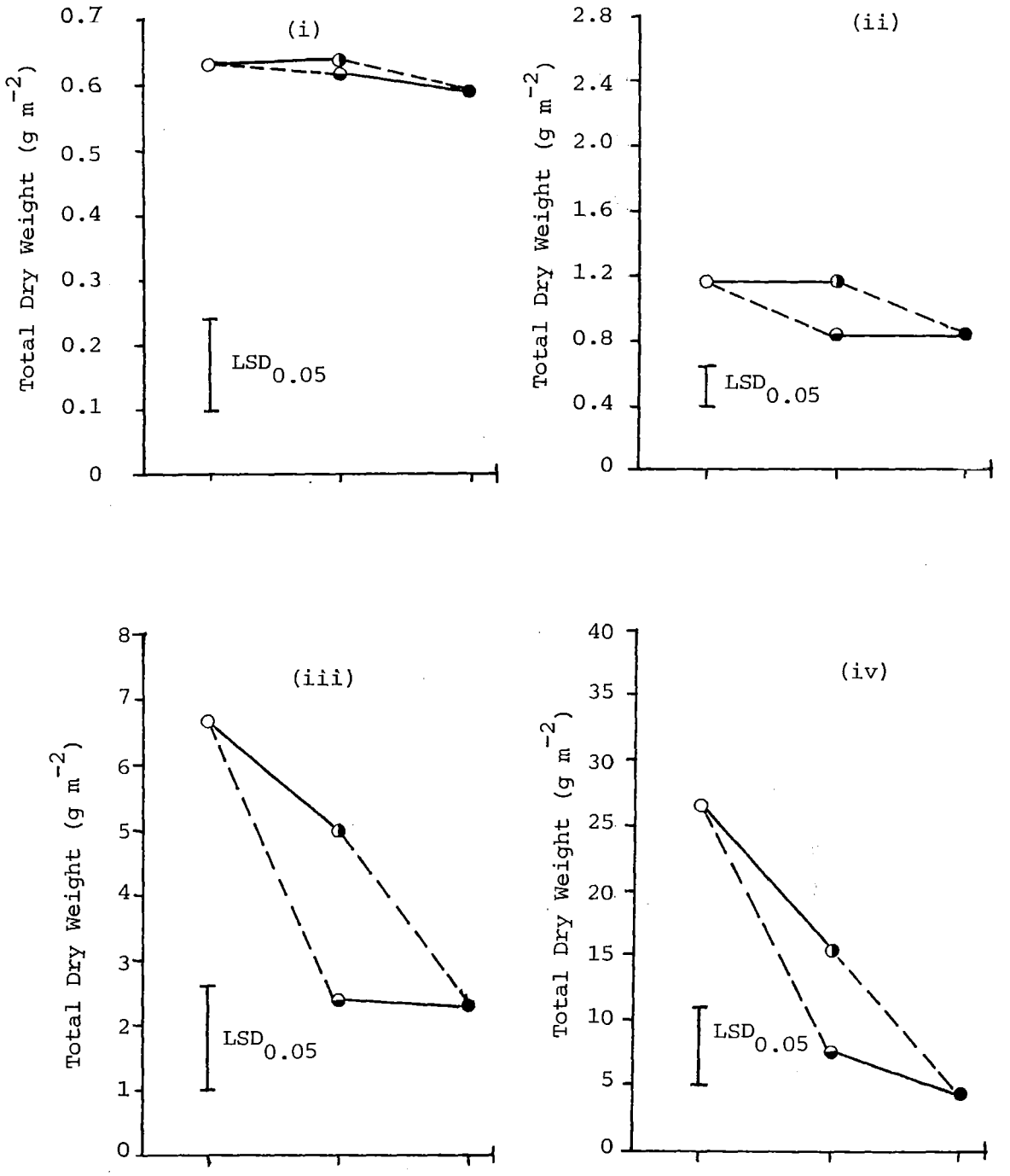
From 35 days after seedling emergence, root interference only and both root and shoot interference (full interference) between yarrow and barley plants significantly decreased the leaf area (LA) of yarrow, compared to when no interference was present (Fig. 5.2b). Though the intensity of shoot interference increased with time, leading to a greater decline in LA of yarrow, its effects were less than in the presence of root interference.

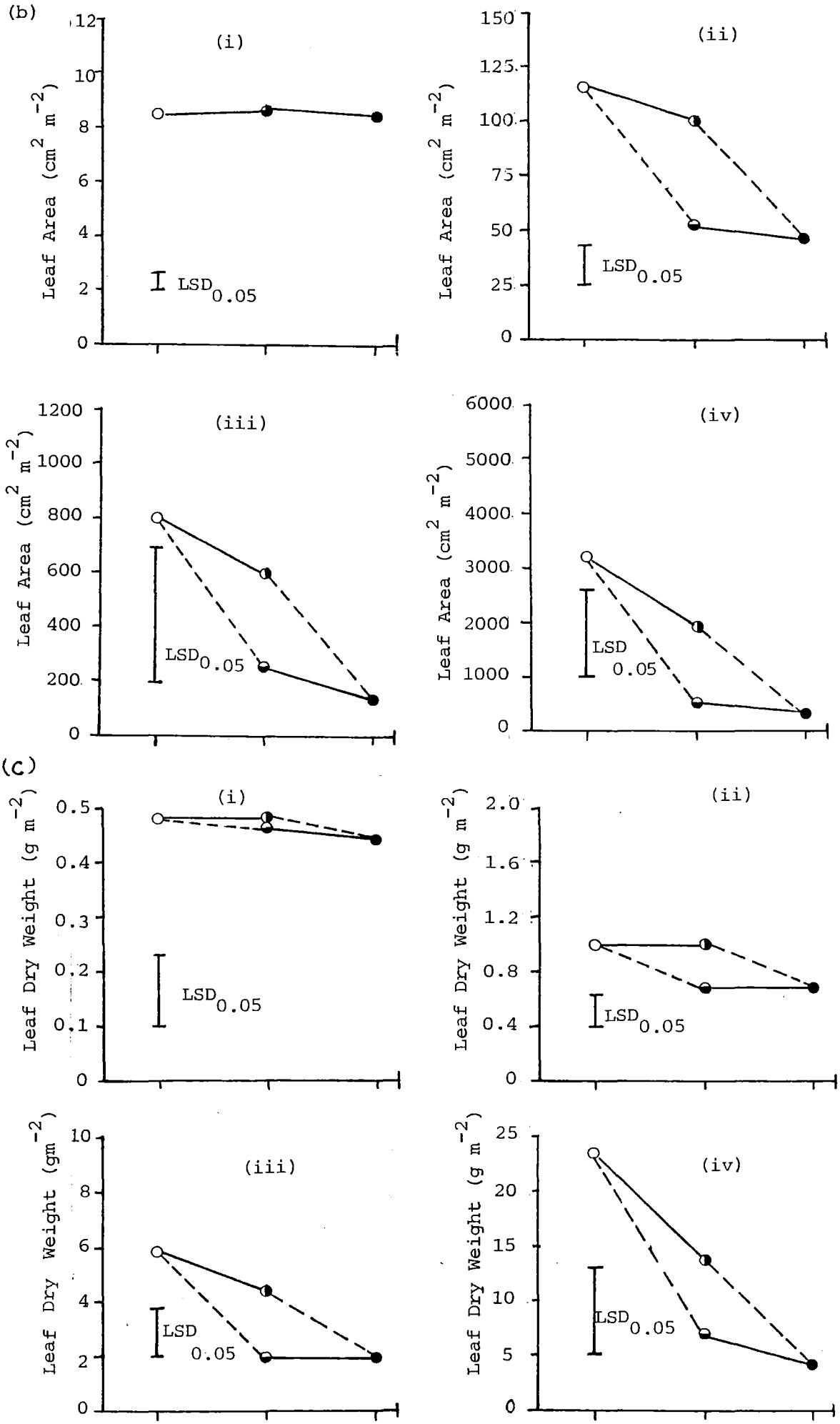
Figure 5.2: Interaction diagrams showing the (a) total dry weight, (b) leaf area, (c) leaf dry weight, (d) stem dry weight, and (e) rhizome dry weight of yarrow.

○ - indicates no interference; ◒ - root interference only; ◑ - shoot interference only; ● - both root and shoot interference.

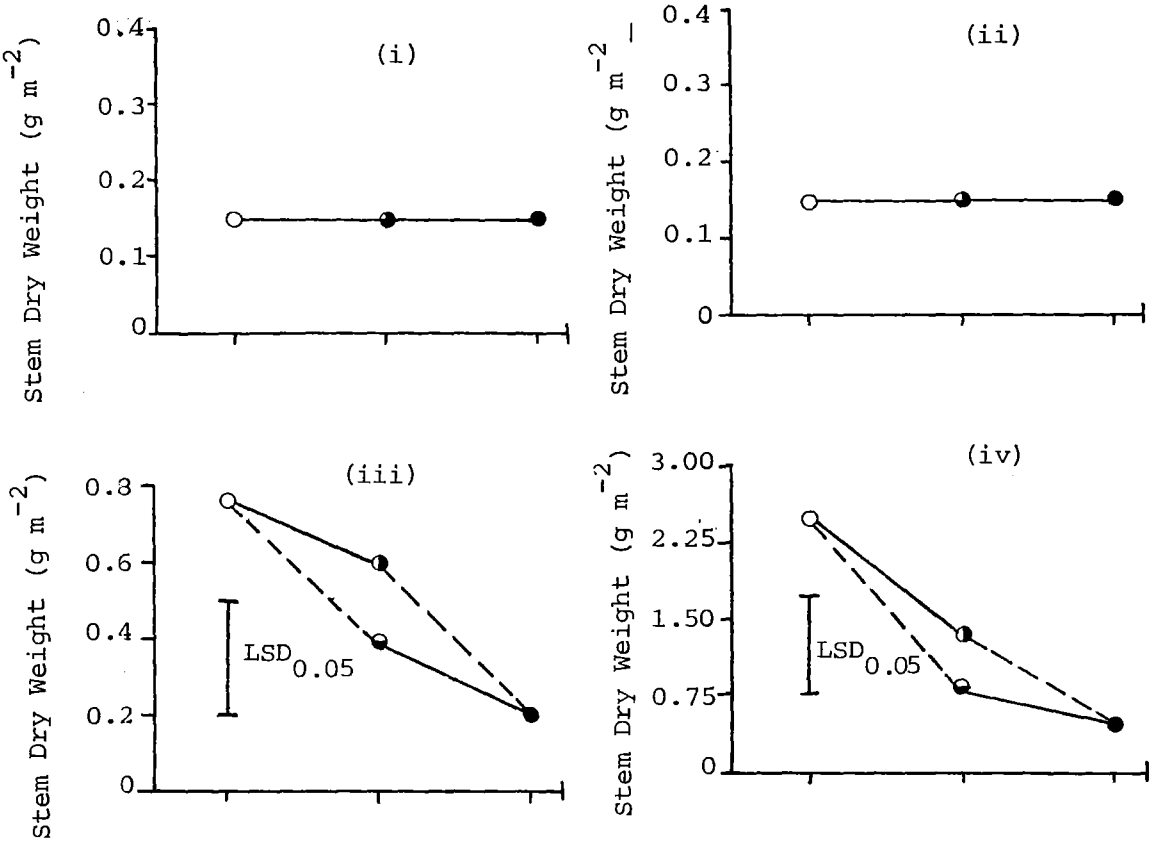
Continuous and broken lines show the influence of introducing shoot and root interference, respectively. In (a), (b), (c) and (d), the diagrams (i), (ii), (iii) and (iv) represent the harvest dates of 21, 35, 49 and 63 days after seedling emergence, respectively; (e) is at 63 days after seedling emergence.

(a)

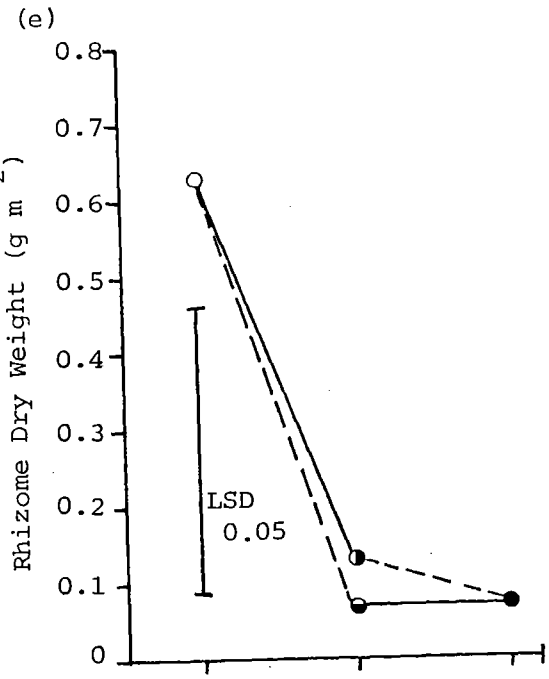

(i)
Total Dry Weight (g m^{-2})
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
LSD$_{0.05}$
(ii)
Total Dry Weight (g m^{-2})
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
LSD$_{0.05}$
(iii)
Total Dry Weight (g m^{-2})
8
7
6
5
4
3
2
1
0
LSD$_{0.05}$
(iv)
Total Dry Weight (g m^{-2})
40
35
30
25
20
15
10
5
0
LSD$_{0.05}$


(b)
(i)
Leaf Area (cm^2 m^{-2})
LSD$_{0.05}$
(ii)
Leaf Area (cm^2 m^{-2})
LSD$_{0.05}$
(iii)
Leaf Area (cm^2 m^{-2})
LSD$_{0.05}$
(iv)
Leaf Area (cm^2 m^{-2})
LSD 0.05
(c)
(i)
Leaf Dry Weight (g m^{-2})
LSD$_{0.05}$
(ii)
Leaf Dry Weight (g m^{-2})
LSD$_{0.05}$
(iii)
Leaf Dry Weight (gm^{-2})
LSD 0.05
(iv)
Leaf Dry Weight (g m^{-2})
LSD$_{0.05}$

(d)


(i)
(ii)
(iii)
(iv)
Stem Dry Weight (g m^{-2})
0.4
0.3
0.2
0.1
0
0.8
0.6
3.00
2.25
1.50
0.75
LSD$_{0.05}$

(e)


Rhizome Dry Weight (g m^{-2})
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
LSD
0.05

In the presence of full interference between the species, the reduction in the LA of yarrow was less than the additive effects when shoot and root interference occurred independently.

5.2.2.3 Total Leaf Dry Weight

The decline in the leaf dry weight (LW) of yarrow occurred earlier in the presence of root interference than in the presence of shoot interference between the species (Fig. 5.2c). From 49 days after emergence, the LW of the yarrow plants in interference with either the roots of barley or in full interference was significantly less than when the two species were not interacting with each other.

5.2.2.4 Total Stem Dry Weight

Up to 35 days after seedling emergence, there was no difference in the stem dry weight (SW) of yarrow whether or not any form of interference occurred between the two species (Fig. 5.2d). Thereafter the SW of yarrow in interference with either the barley roots only or in full interference was significantly less than when there was no interference between the species.

5.2.2.5 Total Rhizome Dry Weight

Rhizomes were present on the yarrow plants only at the final harvest (63 days after emergence) and root or shoot interference from barley significnatly decreased the rhizome dry weight of yarrow (Fig. 5.2e). However, the suppression of rhizome growth in the presence of full interference between yarrow and barley plants was not significantly different from when either the shoot systems or root systems of the two species were in interference.

Experiment 2

Evaluation of the effects of root and/or shoot interference from pea (*Pisum sativum* cv. Huka) plants on the growth and development of seedling yarrow.

5.2.3 Materials and Methods

5.2.3.1 Layout and Experimental Design

Specially designed galvanised iron boxes (0.30 x 0.30 x 0.15 m) with drainage holes at their bases, were divided into self-contained compartments (10 cm wide) using galvanized iron partitions. The aerial partitions were 30 cm in height and were lined with 'Mylar' reflector foil. The above- and below-ground partitions and the rows of yarrow and pea plants were arranged as shown in Figure 5.1.

The Wakanui silt loam soil used in the experiment had 37 parts/10^6 nitrogen (N), and 18 parts/10^6 each of phosphorus (P) and potassium (K); the pH was 6.1. On 15 April 1982, N, P and K were added to the shredded soil at the rate of 357 kg ha^{-1} ammonium sulphate (75 kg ha^{-1} N), 250 kg ha^{-2} Flomaster Super phosphate (20 kg ha^{-1} P) and 125 kg ha^{-1} potassium sulphate (50 kg ha^{-1} K), respectively, and thoroughly mixed. The soil was filled into boxes and sterilized as detailed in Section 5.2.1.1. The boxes were transferred into a glasshouse in which the temperature was controlled (ca. 20°C) and arranged, with the aerial partitions in a north-south direction, in a randomized block design. Each treatment (Fig. 5.1) was replicated 4 times. There were sufficient boxes to enable three sequential harvests of each treatment.

5.2.3.2 Seed Material

Sun dried yarrow seed heads were collected in February 1982 and clean seed was obtained as detailed in Chapter 2. Laboratory germination tests of samples of this seed gave 97% (S.E. 2%) germination. Pea seed was

obtained from a commercial source.

5.2.3.3 Establishment and Management

On 5 May 1982, yarrow seed, imbibed in water and exposed to 3875 lux light intensity (incandescent and fluorescent light from a similar source as detailed in Chapter 2) for 24 h, and pre-germinated pea seed were planted in rows as indicated in Figure 5.1. Three yarrow seeds were placed on the soil surface at each appropriate planting site and covered with a thin layer of soil. The pea seeds were planted 1 cm deep and were inoculated with a peat culture of nitrogen-fixing bacteria recommended for peas (trade name - 'Rhizocote'). In a previous experiment carried out in the field, pea plants nodulated well (Chapter 4). In the present experiment, since the chances of entry of bacteria into the sterilized soil from outside sources was poor (experiment carried out in glasshouse), innoculation of the pea seed was to enable 'effective' nodulation. The spacing between adjacent rows of plants was 10 cm while within the row, they were 5 cm apart.

The seedling plants of yarrow and peas emerged from the soil on 12 May 1982. The yarrow was thinned to one seedling per planting site one week after emergence. The aerial partitions were erected after thinning the yarrow. Irrigation was carried out throughout the experimental period to maintain the soil close to field capacity.

5.2.3.4 Sampling Procedure and Measurements

Each treatment was harvested at 21, 35 and 49 days after seedling emergence. For the same reasons detailed in Section 5.2.1.4, the root fraction was discarded and measurements were carried out only on the shoot system of yarrow. The leaf area, leaf weight and stem weight were measured as detailed in Section 5.2.1.4. There was no rhizome initiation. At the latter two harvests the pea roots had effective nodules.

5.2.3.5 Statistical Analysis

See Section 5.2.1.5 for details.

5.2.4 Results

5.2.4.1 Total Dry Weight

Root interference between yarrow and pea plants significantly decreased the growth of the former species at an earlier stage of its development (i.e., 21 days after seedling emergence) than when only shoot interference was possible (Fig. 5.3a). However, with continued development of both species, the suppression of the growth of yarrow in the presence of shoot interference was significantly greater than when only root interference was present. At all harvests, the greatest retardation in the growth of yarrow occurred when there was full interference between the species. However, this suppression of growth was not as great as the additive effects of root and shoot interference occurring separately.

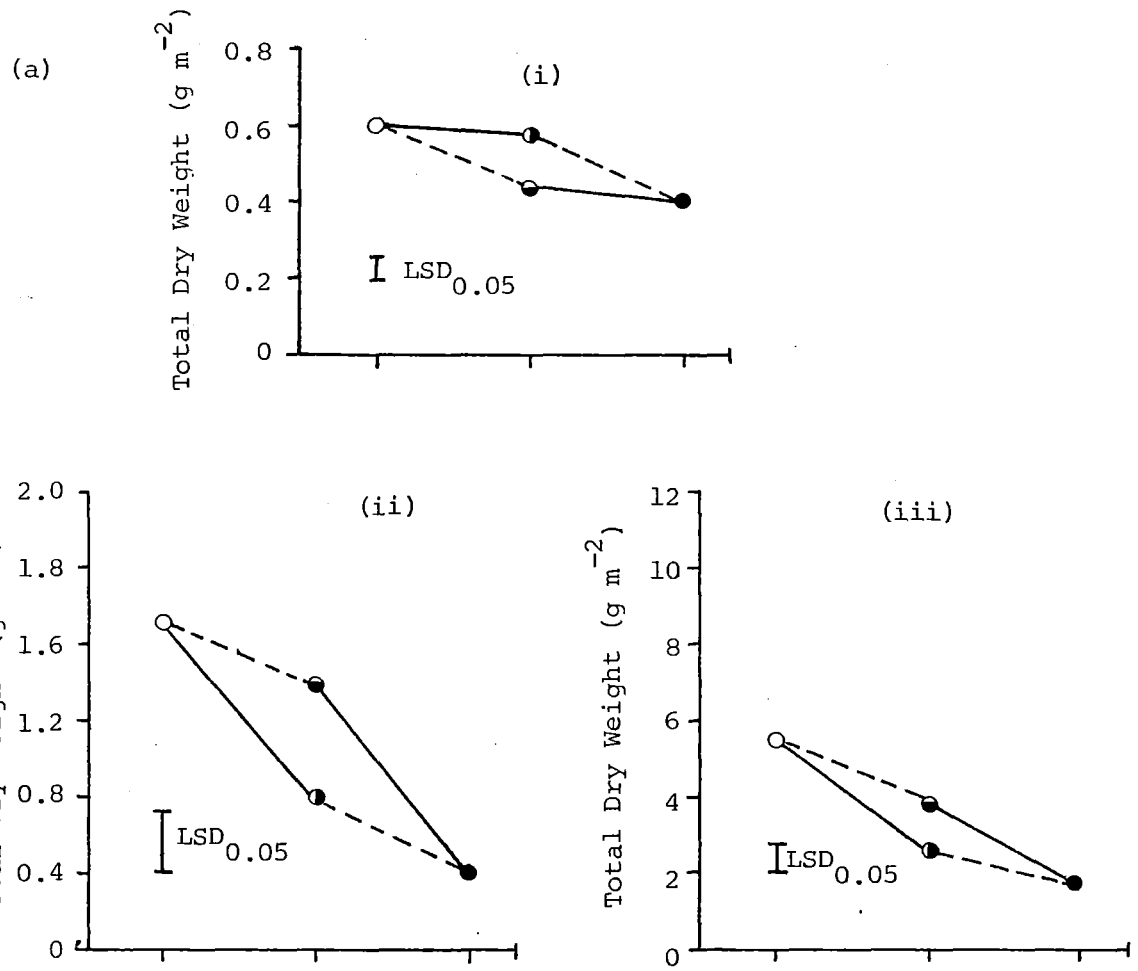
5.2.4.2 Total Leaf Area

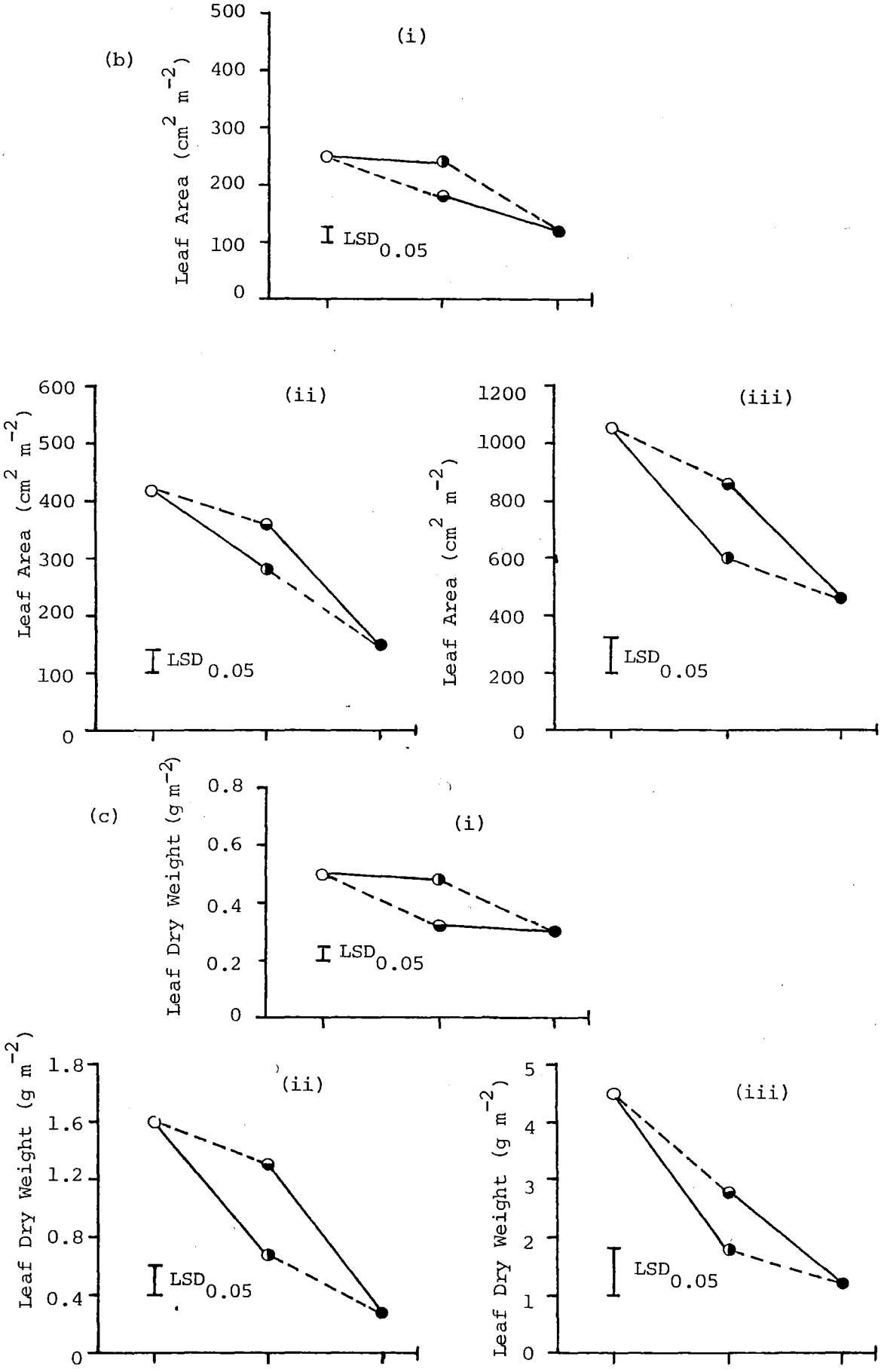
Compared to when no interference occurred between yarrow and pea plants, in the presence of root interference and/or full interference there was a significant decrease in the leaf area (LA) of yarrow from as early as 21 days after seedling emergence (Fig. 5.3b). However, at 35 and 49 days after seedling emergence, shoot interference between the species suppressed the LA of yarrow to a significantly greater degree than root interference. At all harvests, the greatest retardation of LA development in yarrow occurred in the presence of full interference between the species ($P < 0.05$).

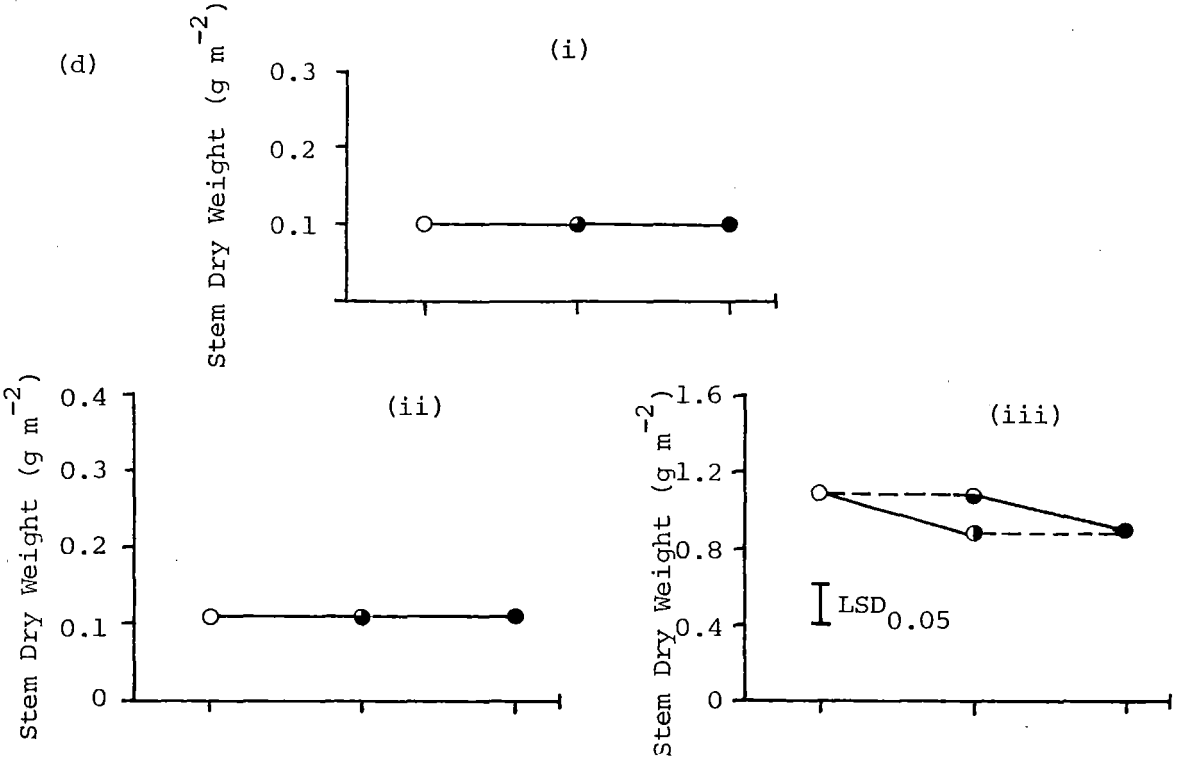
5.2.4.3 Total Leaf and Stem Dry Weights

A significant decline in leaf dry weight (LW) of yarrow occurred earlier (i.e., 21 days after seedling emergence) in the presence of root interference than when only shoot interference occurred between the species (Fig. 5.3c). With further growth and development, shoot interference alone suppressed the LW of yarrow significantly more than root interference.

Figure 5.3: Interaction diagrams showing the (a) total dry weight, (b) leaf area, (c) leaf dry weight, and (d) stem dry weight of yarrow.
○ - indicates no interference; ◒ - root interference only; ◑ - shoot interference only; ● - both root and shoot interference.
Continuous and broken lines show the influence of introducing shoot and root interference, respectively. In (a), (b), (c) and (d) the diagrams (i), (ii), and (iii) represent harvest dates of 21, 35 and 49 days after seedling emergence, respectively.


(a)
(i)
Total Dry Weight (g m^{-2})
0.8
0.6
0.4
0.2
0
LSD$_{0.05}$
(ii)
2.0
1.8
1.6
1.2
0.8
0.4
0
LSD$_{0.05}$
(iii)
12
10
8
6
4
2
0
LSD$_{0.05}$


(b)
(i)
Leaf Area (cm^2 m^{-2})
500
400
300
200
100
0
LSD$_{0.05}$
(ii)
600
500
400
300
200
100
0
(iii)
1200
1000
800
600
400
200
0
(c)
Leaf Dry Weight (g m^{-2})
0.8
0.6
0.4
0.2
1.8
1.6
1.2
5
4
3
2
1


(d)
(i)
Stem Dry Weight (g m^{-2})
0.3
0.2
0.1
(ii)
Stem Dry Weight (g m^{-2})
0.4
0.3
0.2
0.1
0
(iii)
Stem Dry Weight (g m^{-2})
1.6
1.2
0.8
0.4
0
LSD$_{0.05}$

There was no significant difference in the stem dry weight (SW) of yarrow up to 49 days after seedling emergence, whether or not there was interference between yarrow and pea plants (Fig. 5.3d).

Experiments 3 and 4

Some aspects of interaction between yarrow and barley (*Hordeum vulgare* cv. Zephyr) plants (Experiment 3) and yarrow and pea (*Pisum sativum* cv. Huka) plants (Experiment 4) and the aggressivity of yarrow in association with barley or pea plants.

5.2.5 Materials and Methods

5.2.5.1 Layout and Experimental Design

Wakanui silt loam soil was collected in late February 1982 from a field grown in two consecutive crops of wheat; it had 34 parts/10^6 nitrogen (N) and 15 parts/10^6 each of phosphorus (P) and potassium (K) and a pH of 6.1. The shredded soil was sterilized with methyl bromide gas as detailed in Chapter 4. To a quantity of soil sufficient to fill 60 plastic containers of 5 *l* capacity each, N, P, and K were added at rates equivalent to 357 kg ha^{-1} ammonium sulphate (75 kg ha^{-1} N), 250 kg ha^{-1} Flomaster superphosphate (20 kg ha^{-1} P), and 125 kg ha^{-1} potassium sulphate (50 kg ha^{-1} K) respectively, and mixed thoroughly. The soil was filled into the containers and lightly compacted; 30 containers were used for Experiment 3 while the remaining 30 containers were used for Experiment 4.

The containers were transferred into a glasshouse, where the temperature was maintained at approximately 20^{o}C, and arranged in randomized block designs; the containers in each experiment were in two separate locations in the glasshouse.

The treatments in each experiment (Fig. 5.4) were replicated 6 times. The adjacent treatments in each replicate were spaced 0.5 m apart while each replicate was separated by a 0.75 m border strip.

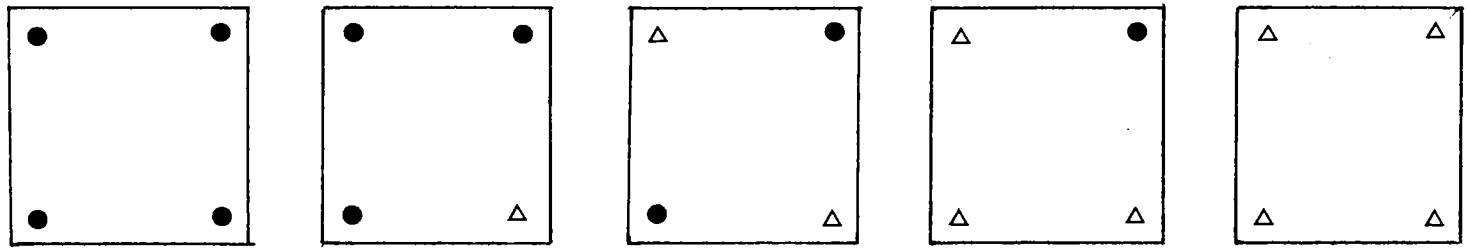
5.2.5.2 Seed Material

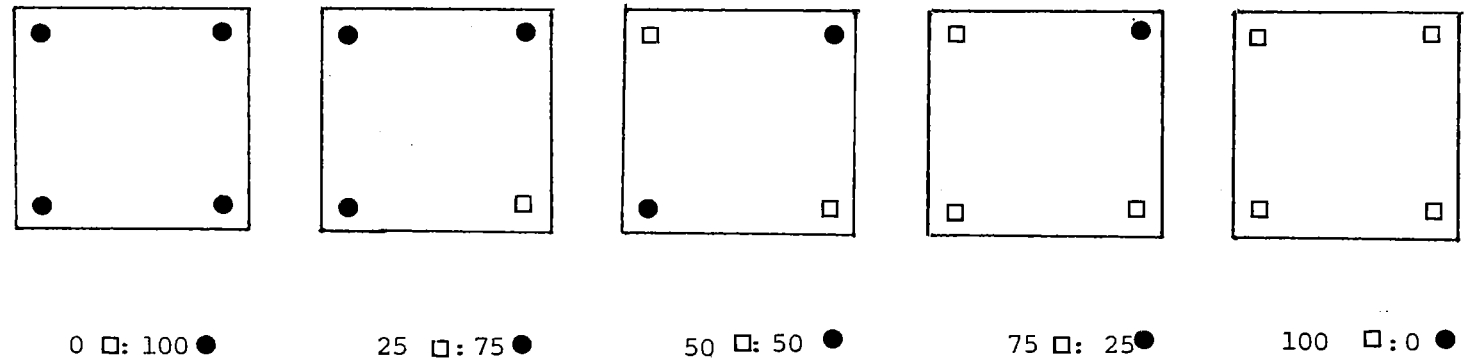
Yarrow seed heads which had sun-dried were collected in February 1982 and seed cleaning was carried out as detailed in Chapter 2. The barley and pea seeds were obtained from a commercial source.

5.2.5.3 Establishment and Management

On 1 March 1982, pre-germinated yarrow, barley, and pea seed were planted as indicated in Figure 5.4. Two yarrow seeds were placed on the soil surface and a single barley (Experiment 3) or pea (Experiment 4) seed was planted at 1 cm depth, at each of their respective planting sites. One week later, when the plants had established, the yarrow was thinned to one seedling per site. Immediately after thinning the yarrow, a peat culture of nitrogen-fixing bacteria (trade name: 'Rhizocote'), specially recommended for peas, was added to the soil surface of each treatment in Experiment 4 and watered into the soil (refer Section 5.2.3.3). In order to minimize lateral illumination, which is rarely experienced by plants in the field, white plastic shields, with their inner surfaces lined with black polythene, were placed around each container and adjusted regularly to the height of the tallest plant. The soil in each experiment was maintained close to field capacity throughout the experiment.

Figure 5.4: Treatments in the yarrow/barley (Experiment 3) and yarrow/pea (Experiment 4) replacement series experiments. The symbol ● denotes a yarrow plant; △ denotes a barley plant; □ denotes a pea plant.





5.2.5.4 Sampling Procedure and Measurements

On 22 April 1982, 49 days after seedling emergence from the soil, the aerial parts of yarrow and barley plants (Experiment 3) and yarrow and pea plants (Experiment 4) in each treatment were harvested separately and dried to a constant weight at 80°C to determine their respective dry weights. The roots were not included for reasons detailed in Section 5.2.1.4. The roots of the pea plants had effective nodules. The shoot material of each species, from each treatment, was separately milled into a fine powder in a 'Cyclone' grinder and chemically analysed to determine N, P, and K levels. Kjeldahl digestion followed by auto-analysis of N, colorimetric determination of P, and flame emission spectrometric determination of K were carried out. The procedures used in the chemical analysis are given in Appendix 16.

In each experiment the relative yields (r) of yarrow and the crop species and their relative yield totals (RYT) for total weight, nitrogen, phosphorus, and potassium, were calculated using the method of Hall (1974a; refer Section 5.1). The aggressivity of yarrow (competitive ability) at each relative density of barley or pea plants was calculated using the method of McGilchrist and Trenbath (1971; refer Section 5.1).

5.2.5.5 Statistical Analysis

When two plant species are grown both in monocultures and in mixtures of the species in replacement series type of arrangement, their respective relative yields, when presented in a replacement diagram, follow linear trends (analogous to Raoult's Law; each linear curve has a slope of 45°) when there is no interference between the species (De Wit, 1960; Hall, 1974a). A linear trend (linear curve which has zero

slope) in the relative yield total of two species growing in association at different relative densities indicates that they are mutually exclusive (De Wit and Van den Bergh, 1965); that is, there is either no interference between the species or the reduction in the relative yield of one species is compensated by an equal increase in the relative yield of the other species.

In the present replacement series study involving yarrow and barley plants (Experiment 3) or yarrow and pea plants (Experiment 4), analysis of variance of the orthogonal regression components of the relative yields of dry weight (r_W), nitrogen (r_N), phosphorus (r_P) and potassium (r_K) of each species were carried out separately. In each analysis the different relative densities of the species were the treatments. A significant deviation from the linear trend of relative yield indicated the presence of interference. Separate analyses of variance of the orthogonal regression components of the relative yield totals of dry weight (RYT_W), nitrogen (RYT_N), phosphorus (RYT_P), and potassium (RYT_K) were carried out, in each experiment. A significant deviation from the linear trend of relative yield total indicated that the two species (i.e., the yarrow and barley plants or yarrow and pea plants) were not mutually exclusive.

A separate analysis of variance was carried out on the 'Aggressivity' data of yarrow in each experiment.

5.2.6 Results

5.2.6.1 Relative Yield and Relative Yield Total

The per plant yields of dry weight, nitrogen, phosphorus and potassium of yarrow were reduced in mixtures with barley or pea plants compared to when the yarrow was in monoculture (Appendix 17). The converse was true for the barley or pea plants grown in association with

yarrow. Owing to the difficulty involved in comparing the performance of the different species in absolute yields (van den Bergh, 1968), the changes in the yields of dry weight, nitrogen, phosphorus and potassium in each species were mathematically described by calculating their appropriate relative yields on a per stand basis (Hall, 1974a).

The trends in the relative yields of dry weight (r_W), phosphorus (r_P) and potassium (r_K) of yarrow and barley plants deviated significantly from their respective linear trends (refer Section 5.2.5.5) when the two species were grown in association (Appendix 18; Fig. 5.5). The presence of barley plants in association with yarrow plants resulted in the reduction in the r_W, r_N, r_P and r_K of the latter species; the converse was true for the barley plants. However, the decrease in the r_W of yarrow in association with barley was greater than the corresponding increase in the r_W of barley (Fig. 5.5). This resulted in the significant deviation of the relative yield total of dry weight (RYT_W) from the linear trend (Appendix 19; Fig. 5.5). The RYT_W of yarrow and barley grown in association was < 1. The decreases in the r_N, r_P and r_K of yarrow grown in association with barley were compensated for by corresponding increases in their respective relative yields in barley (Fig. 5.5). Therefore, the trends in relative yield totals of nitrogen (RYT_N), phosphorus (RYT_P), and potassium (RYT_K) were not significantly different from their appropriate linear trends (Appendix 19; Fig. 5.5).

When yarrow plants and pea plants were grown in association their respective r_W, r_N, r_P, and r_K, deviated significantly from their appropriate linear trends (Appendix 18; Fig. 5.6). The r_W, r_N, r_P and r_K were decreased for yarrow and increased for the pea plants when the two species were grown together (Fig. 5.6). However, the decreases in the r_W and r_N of yarrow in association with the pea plants were less than the corresponding increases in their respective relative yields in the pea plants (Fig. 5.6). This resulted in the significant deviation of

Figure 5.5: Replacement series diagram in which the relative yields (r_y; r_b) of dry weight (——), nitrogen (----), phosphorus (-·-·-) and potassium (-···-) for yarrow (species y) and barley (species b) and their relative yield totals ($r_y + r_b$) are plotted against the relative density (Z_y; Z_b) of each species. The dotted lines for r_y and r_b are their expected linear trends in the absence of interference between the two species. The linear trend of $r_y + r_b$ which is expected when there is either no interference between yarrow and barley plants or when the two species are mutually exclusive is indicated by a dotted line.

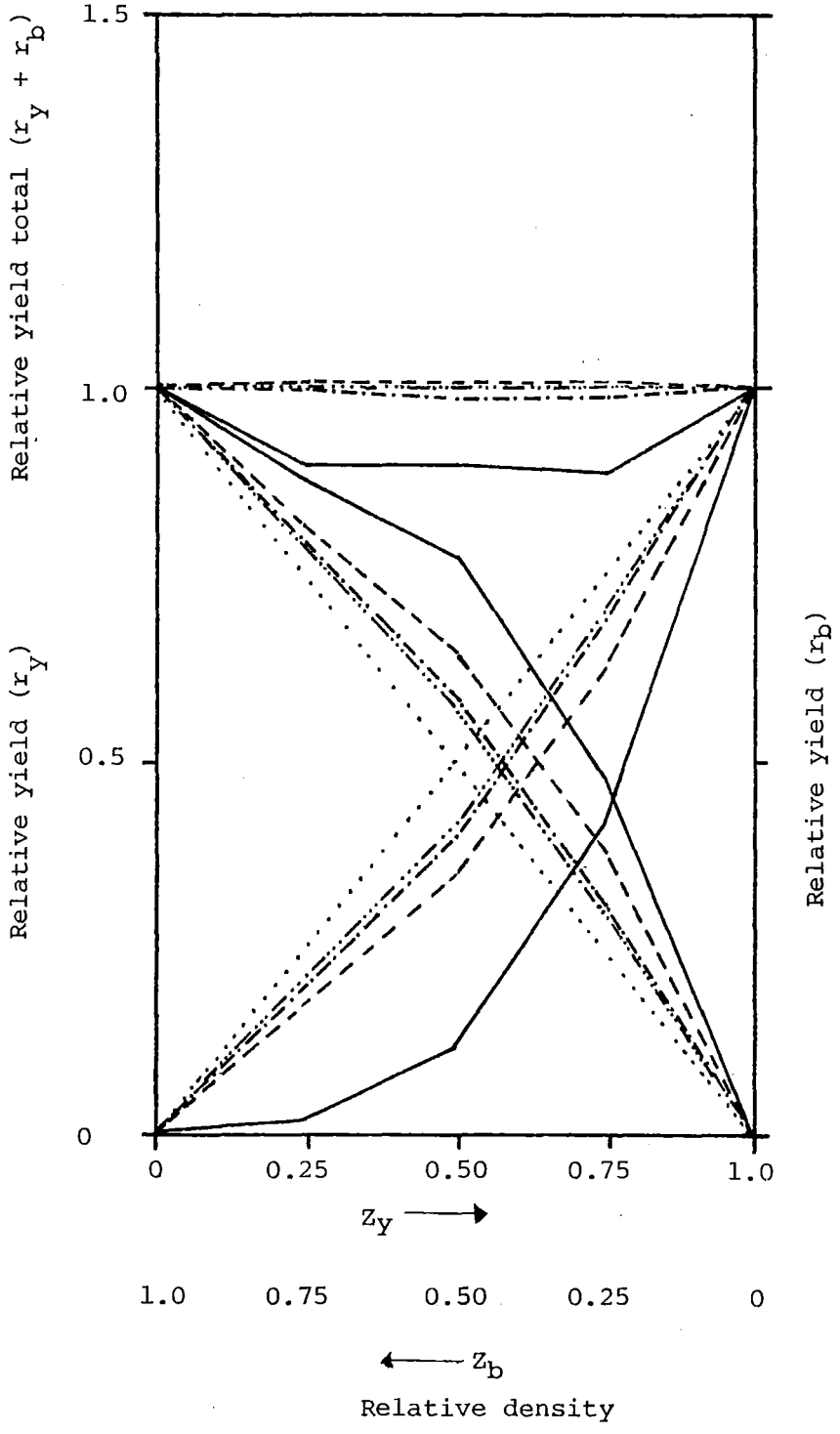
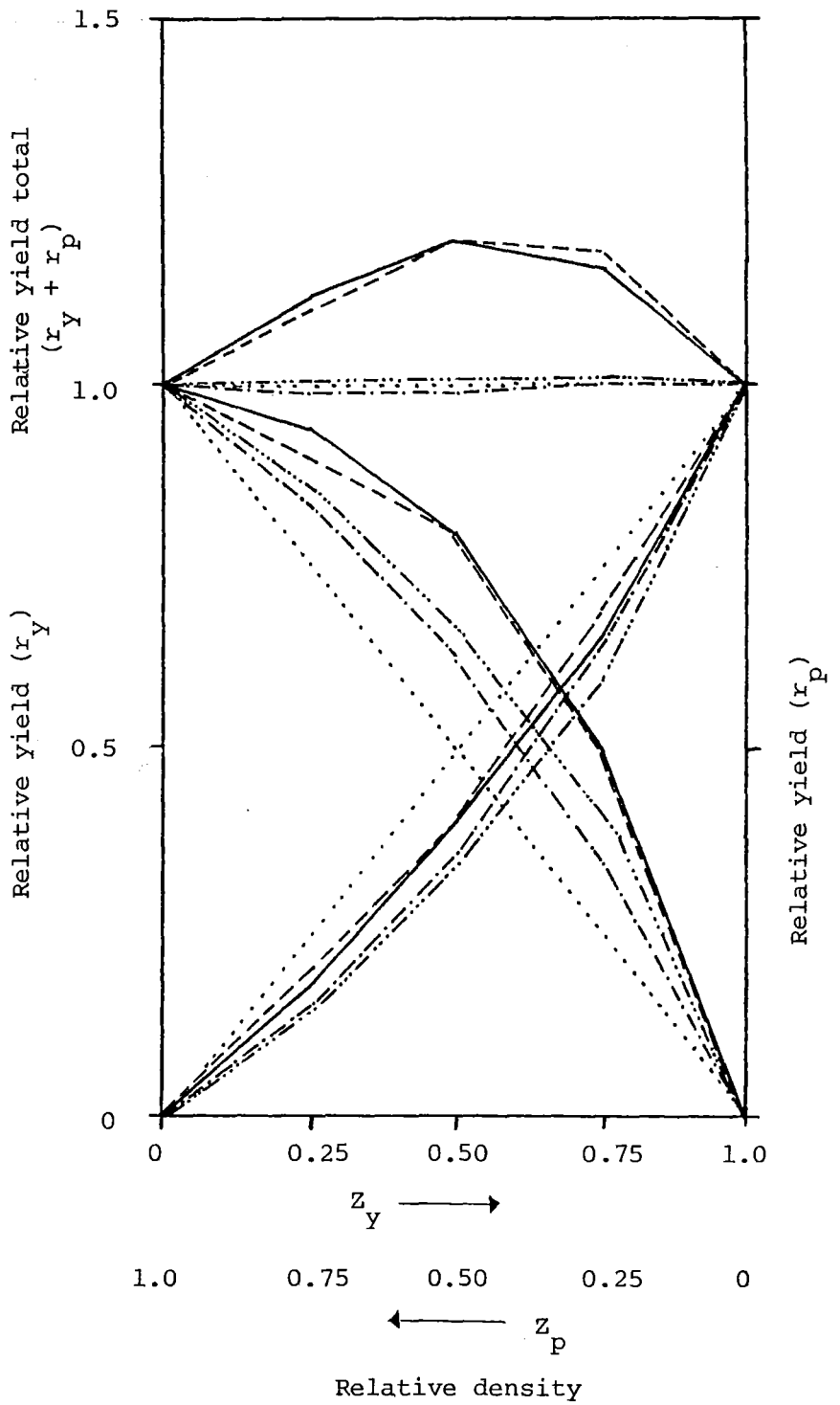

Relative yield total ($r_y + r_b$)
1.5
1.0
0.5
0
Relative yield (r_y)
Relative yield (r_b)
0
0.25
0.50
0.75
1.0
z_y
1.0
0.75
0.50
0.25
0
z_b
Relative density

Figure 5.6: Replacement series diagram in which the relative yields (r_y; r_p) of dry weight (——), nitrogen (----), phosphorus (-·-·-) and potassium (←··-··) for yarrow (species y) and pea plants (species p) and their relative yield totals ($r_y + r_p$) are plotted against the relative density (Z_y; Z_p) of each species. The dotted lines for r_y and r_p are their expected linear trends in the absence of interference between the two species. The linear trend of $r_y + r_p$ which is expected when there is either no interference between yarrow and pea plants or when the two species are mutually exclusive is indicated by a dotted line.


1.5
1.0
0.5
0
Relative yield total
$(r_y + r_p)$
Relative yield (r_y)
Relative yield (r_p)
0
0.25
0.50
0.75
1.0
z_y
1.0
0.75
0.50
0.25
0
z_p
Relative density

their trends in RYT_W and RYT_N from the linear trend (Appendix 19; Fig. 5.6). The RYT_W and RYT_N were > 1 when yarrow and pea plants were grown in association. The trends in RYT_P and RYT_K were not significantly different from their respective linear trends.

5.2.6.2 Aggressivity of Yarrow

The aggressivity (competitive ability) of yarrow grown in association with barley was low at all relative densities of the latter species (Table 5.1). With the increase in the relative density of barley there was a significant decline in the aggressivity of yarrow. Similarly, when grown in association with pea plants, the aggressivity of yarrow was low at all relative densities of the former species and significantly decreased as the relative density of pea plants increased (Table 5.1).

Table 5.1: The aggressivity of yarrow[#] in association with different relative densities of barley or pea plants. Each value is a mean of 6 replicates.

Relative Density of Crop Species (Z)	Aggressivity
(i) Barley plants	
0.25	-0.60
0.50	-0.72
0.75	-0.82
$LSD_{0.05}$	0.08
CV (%)	14.73
(ii) Pea plants	
0.25	-0.31
0.50	-0.44
0.75	-0.63
$LSD_{0.05}$	0.11
CV (%)	19.43

[#]Forty-nine days after seedling emergence.

5.3 DISCUSSION

The majority of studies carried out to separately evaluate the effects of shoot and root interference between different plant species, including *Lolium perenne* and *Phalaris tuberosa* (Donald, 1958), *Dactylis glomerata* and *Holcus lanatus* (Remison and Snaydon, 1980), and *Hordeum vulgare* and *Vicia faba* (Martin and Snaydon, 1982), have shown that root interference commenced earlier than shoot interference and continued to be of greater importance than shoot interference at least during the period of early vegetative growth and development. It has been suggested that this is possibly due to their root systems extending and intermingling before the shoot systems interact with each other and/or that soil factors more commonly limit the growth and development of plants than does light (Milthorpe, 1961; King, 1971). In the present study, root interference between yarrow and barley plants markedly suppressed the growth and development of yarrow before shoot interference between the two species had a similar effect and it continued to be of greater importance than shoot interference up to the time when the experiment was terminated at 63 days after seedling emergence (Fig. 5.2). Thus these results on interference between yarrow and barley plants are in agreement with the generally observed trend in interference between two plant species that was detailed above. Similarly, root interference between yarrow and pea plants markedly suppressed the growth and development of the former species earlier than when only the shoot systems of the two species were allowed to interact (Fig. 5.3). However, with further time (i.e ., at 35 and 49 days after seedling emergence) it was observed that shoot interference between yarrow and pea plants was more important than root interference in suppressing the growth and development of the yarrow. This result contradicts the finding by several other workers that root interference between different plant species continues to be of greater importance than shoot interference at least during the first few months after seedling emergence

(e.g. Aspinall, 1960; Remison and Snaydon, 1980). The reason(s) for this observed difference clearly requires further explanation. Some workers have stated that during the early stages of growth and development the nitrogen fixed by leguminous species is not available to other species growing in close proximity (Hall, 1974a; Harper, 1977). Therefore, when the roots of yarrow and pea plants initially intermingled, it is unlikely that the former species would have had access to the nitrogen which was symbiotically fixed by the pea plants. However, it has been suggested that the ability of leguminous species to symbiotically fix nitrogen decreases their dependence on the mineral nitrogen present in the soil and thereby leaves more of the soil nitrogen to be utilized by any non-leguminous species growing in close proximity to them (De Wit *et al.*, 1966; Martin and Snaydon, 1982). This would undoubtedly decrease the competitive interference between the leguminous and non-leguminous species for soil nitrogen. Thus there may have been a decrease in interference between the yarrow roots and nodulated pea roots for soil nitrogen when they were intermingled. The increased shading of the yarrow canopy by the pea canopy and the decreased interference between the root systems of the two species for soil nitrogen may have been principally responsible for the greater importance of shoot interference compared to root interference in suppressing the growth and development of yarrow at 35 and 49 days after seedling emergence (Fig. 5.3).

The results from the above experiments showed that the relative importance of either shoot interference or root interference between plants can vary depending on the species involved. Therefore, a generalized statement that root interference between plant species is more important than shoot interference during the first few months of growth and development of seedling plants (Remison and Snaydon, 1980) does not appear to be always applicable. Schreiber's (1967) finding that shoot interference between *Amaranthus retroflexus* and *Lotus corniculatus* is more important than

root interference between the two species in suppressing the growth of the latter species further supports the above argument.

When the shoot and root systems of yarrow and barley plants or yarrow and pea plants were allowed to intermingle (full interference), the suppression of the growth and development of yarrow was greater than when either their respective shoot systems or root systems were allowed to interact (Figs. 5.2, 5.3). However, the suppression of yarrow in full interference with barley or pea plants was not additive. That is, the reduction in the growth and development of yarrow in full interference with barley or pea plants was less than the sum of the reductions when shoot interference or root interference occurred separately, indicating that there were interactions between shoot and root interference. The nature of these interactions was not evaluated in the present study. Similar findings of non-additivity of the separate effects of shoot and root interference between different plant species have been reported by other workers (e.g. Donald, 1958; Aspinall, 1960).

Plant species growing as neighbours competitively interfere with each other for incident light, water and mineral nutrients necessary for their growth and development (Clements *et al.*, 1929; Donald, 1963; Haynes, 1980). It is also possible that non-competitive interference, including allelopathic interactions (e.g. McPherson and Muller, 1969; Putnam and Duke, 1974; Kimber, 1973); the greater availability of mineral nitrogen to non-leguminous species growing in association with nodulated leguminous species (e.g. De Wit *et al.*, 1966; Hall, 1974b; Martin and Snaydon, 1982); the transfer of symbiotically fixed nitrogen from leguminous species to non-leguminous species (e.g., Harper, 1964; Haynes, 1980), can occur between some plant species. The competitive interference between the shoot systems of plant species is principally for incident light. When the root systems of plant species intermingle

competitive interference for water and nutrients and non-competitive interference can occur simultaneously.

Owing to a relatively taller and more spreading growth habit of the barley and pea plants compared to the prostrate rosette-like nature of the yarrow plants, it is likely that the latter species would be shaded by either of the two former species when they grow in close proximity. This was evident in previous studies carried out in the field (Appendix 7). It was also observed that the decreased availability of incident light suppressed the growth and development of seedling yarrow plants (Tables 3.1, 3.2, 3.4). Therefore, it can be presumed that interference for incident light was an important factor responsible for the suppression of the growth and development of seedling yarrow grown in full interference with barley or pea plants (Figs. 5.2, 5.3).

In addition to the interference for incident light, the marked deviations in the relative yields of nitrogen (r_N), phosphorus (r_P) and potassium (r_K) of yarrow and barley plants or yarrow and pea plants from their respective linear trends, when grown in mixtures (Figs. 5.5 and 5.6; Appendix 18), indicated that there was competitive interference between the appropriate species for the available soil N, P and K (refer Section 5.2.5.5). The presence or absence of interference for other 'mineral' nutrients between yarrow and barley plants or yarrow and pea plants was not evaluated. In the present replacement series experiments adequate water was supplied to the soil to maintain it at field capacity (Section 5.2.5.3). Therefore, it is unlikely that there would have been interference for water between yarrow and the associated barley or pea plants. However, under field conditions, where the soil moisture level can fluctuate rapidly over short time periods, interference for soil moisture between yarrow and barley or pea plants is a possibility.

When the relative yield total (RYT) of two plant species growing in association is 1.0 it indicates that they are competitively interfering

with each other for the same growth factors or that there is no interference between them (De Wit and Van den Bergh, 1965). However, there are instances when the presence of one species either restricts or promotes the growth and development of another species due to non-competitive interference between them (Harper, 1964). When there is a restriction of growth and development of a species by another species their RYT is < 1.0 while the promotion of growth and development of a species by another species results in their RYT being > 1.0 (De Wit, 1960). This transgressive yielding of a mixture of two species has been described as 'underyielding' (i.e. RYT < 1.0) and 'overyielding' (i.e., RYT > 1.0) (Trenbath, 1974).

When yarrow and barley plants were grown together their relative yield total of dry weight (RYT_W) markedly 'underyielded' (Fig. 5.5; Appendix 19). This indicated that there was non-competitive interference between the yarrow and barley plants in addition to the above detailed competitive interference between these two species for light and soil N, P and K. The per plant yields of dry weight of yarrow and barley grown in mixtures, at different relative densities of the two species, indicated that the growth of yarrow was suppressed in the presence of barley plants while the converse did not occur (Appendix 17). In a previous study, it was observed that even though adequate amounts of light, water and mineral nutrients were supplied to barley and *Stellaria media* plants growing in association, the former species suppressed the growth of the latter species (Overland, 1966). She attributed this to the allelopathic effect of the alkaloid substances exuded from the roots of the barley plants. Similarly, in the present study, the allelopathic effect of barley plants on the yarrow plants growing in its vicinity may have been primarily responsible for the observed non-competitive interference between these two species.

The relative yield total of dry matter of yarrow and pea plants markedly 'overyielded' when the two species were grown in mixture (Fig. 5.6; Appendix 19) and indicated that they were, at least partially, utiliz-

ing different environmental resources (De Wit, 1960). The 'overyielding' of the relative yield total of nitrogen when yarrow and pea plants were grown in mixture (Fig. 5.6; Appendix 19) showed that the two species were obtaining this nutrient from different sources. The most likely explanation for this is that the presence of effective root nodules on the pea plants would have enabled them to obtain nitrogen by symbiotic fixation, thus leaving more of the soil nitrogen to be utilized by the yarrow plants. A similar conclusion was reached by other workers for the observed 'overyielding' between graminous and leguminous species grown in mixture (e.g., De Wit *et al.*, 1966; Hall, 1974a; Martin and Snaydon, 1982). It is also possible that the greater seedling vigour of the pea plants compared to the yarrow plants (refer Chapter 4, Fig. 4.1) would have resulted in the two species utilizing environmental resources, especially soil nutrients, at different times. In other studies with cereal-legume mixtures, the 'overyielding' of the relative yield totals were said to be due to the species using resources at different times (e.g., Osiru and Willey, 1972, 1976). However, in the present study, the presence or absence of spatial differences in nutrient uptake were not evaluated.

The aggressivity (competitive ability) of different plant species growing in association is dependent on many characteristics, including seed size (Black, 1957, 1958), seedling vigour (Laskey and Wakefield, 1978), canopy height (Harper, 1964), leaf area (Norman *et al.*, 1971), rate of stem elongation in response to shading (Williams, 1964), shade tolerance (Langer, 1973), rate of root growth and development (Harris, 1967), rate of uptake of water and mineral nutrients (Bowen, 1973; Cohen, 1970), and the ability to fix nitrogen symbiotically (Vallis, 1978). The relatively small seed size of the yarrow compared to the barley or pea seeds (Section 4.4); the low seedling vigour of yarrow in relation to the barley or pea seedlings (Fig. 4.1); the prostrate rosette-like growth habit of the yarrow plants compared to the taller and more spreading nature of the barley or pea

plants; lower leaf area of the yarrow canopy in relation to the leaf area of barley or pea plants (Fig. 4.3) and the inability of its stem to elongate in response to shading before flower initiation (Bourdot, 1980); the suppression of the growth and development of yarrow in shade (Tables 3.1, 3.2 and 3.4); the reduced availability of soil N, P and K to yarrow plants growing in association with the barley or pea plants (Figs. 5.5, 5.); and the suppression of the growth of yarrow plants by allelopathic influences of the barley plants (Fig. 5.5) are undoubtedly some of the factors responsible for the low aggressivity of yarrow grown in association with the barley and pea plants (Table 5.1).

CHAPTER 6

GENERAL DISCUSSION

Since the inception of crop farming, weeds growing among cultivated species have brought about losses in the economic yield of plants. In attempts to overcome the problems caused by weeds, various manual, mechanical, cultural, biological, and chemical techniques or different combinations of them have been developed and used to exert such pressures that the growth and development of the economically useful species is favoured over that of the weed species. Until the early 1950's, these weed management techniques were generally applied without a clear understanding of the biology of the weed species. Chancellor (1968) emphasised the need to understand the points of strength and frailties of the weed species in order to exploit their weaknesses. He stated that such an approach would shorten the 'endless road' to effective and long-term management of weeds and also enable the development of completely new techniques to be used in the war against problem weeds. In recent times, weed scientists have realized the importance of such an approach and many studies on different aspects of the biology of weeds have been carried out (e.g., Harper, 1959; Thurston, 1961; Chancellor, 1970; Hill, 1977).

Yarrow, which was a component in mixtures of species used in the development of high country pastures in New Zealand, spread to arable land and has since become a problem weed in many crops, including beans (*Phaseolus vulgaris*), field peas (*Pisum sativum*) and beet (*Beta vulgaris*) and in white clover (*Trifolium repens*) grown for seed (Bourdot *et al.*, 1979; Bourdot and Butler, 1981). It is a perennial species which has the ability to regenerate from seeds as well as from rhizome buds (Korsmo,

1954; Reynolds, 1961). Although the relative importance of the sexual and vegetative methods of reproduction are likely to vary depending on such factors as seeding history and the time and depth of soil cultivation, many workers believe that yarrow plants formed from rhizome fragments are almost always of major significance as a weed problem in crops (Hilgendorf and Calder, 1952; Bourdot and Butler, 1981). However, it has been observed that in certain instances the seedling yarrow plants are more detrimental to crops than the yarrow plants establishing from rhizome fragments (Field, personal communication). This is due mainly to the difficulties involved in planning and carrying out effective control measures before the actual density of the seedling yarrow population is observed in the crop and the limitations of the post-crop emergence control measures that are available, including the lack of suitable selective post-emergence herbicides.

Although yarrow has been recognized as a problem weed in arable land in Canterbury, New Zealand, for several decades (Hilgendorf and Calder, 1952), it was only recently that detailed studies of the biology of this species were carried out (Bourdot, 1980, 1982; Bourdot, Field and White, 1982). However, these studies were mainly on the growth and development of the rhizome system of yarrow, while in the present study, some aspects of the biology of the seeds and seedlings of the species were evaluated.

This final discussion attempts to co-ordinate the current knowledge on the biology of the seeds, seedlings and the rhizomes of yarrow and to determine the persistance and aggressivity characteristics of the species as a weed in arable crops. Some of the current information is directly applicable to formulating control strategies for the weed.

The persistance of weed species is dependent on many of their inherent characteristics, some of which were identified by Sagar (1968). The following is a generalized list of some of the characteristics that

determine the persistance of weed species and a description of the present knowledge on the persistance of yarrow:

(i) Quantity of seed produced.

(ii) Dispersal and dormancy of seeds.

(iii) Survival of seeds in the soil and depth of emergence of seedlings.

(iv) Periodicity of germination of seeds (season).

(v) Seedling adaptability to changes in the environment.

(vi) Ability to reproduce vegetatively.

(vii) Seasonal variations in the growth and development of the vegetative reproduction system.

(viii) Dormancy and survival of the vegetative buds in the soil.

(ix) Seasonal patterns of new shoot production from vegetative buds.

In the field situation, pure stands of rhizomatous and seedling yarrow were estimated to produce approximately 900,000 and 243,000 seeds m^{-2}, respectively, in a single season of sexual reproduction (Bourdot *et al.*, 1979; Appendix 14). Owing to the light weight and small size of the yarrow seed (Appendices 6, 13), they are likely to be wind-blown for short distances from the parent plants while some seed may be dispersed over a wider area by their entanglement in sheep's wool (Reynolds, 1961). However, since the seeds do not possess special structures to aid in wind dispersal (Appendix 13, Plate 1) and are known to have poor aerodynamic efficiency (Bostock, 1978), it is not unreasonable to presume that most of them are shed close to the plants on which they are produced. If the land is subsequently cultivated it would result in large quantities of yarrow seed being incorporated into the soil. Roberts (1966) reported that when the seeds of different plant species present in the soil seed-bank were encouraged to germinate by regular cultivation of the soil, it took approximately seven years to reduce the seed population to 1% of its

original level, provided further seeding was prevented. Therefore, one season of seeding of a yarrow population present on arable land would substantially enhance the persistance of the species.

The light weight and small size of the individual yarrow seeds (Appendices 6, 13) indicates that they have a low amount of embryonic capital. Therefore, it is essential that they germinate on or near the soil surface for successful seedling establishment to occur. Furthermore, owing to the small seedling size at emergence (Kannangara, unpublished) and the prostrate vegetative growth habit of yarrow (Appendix 13) it is important that their seeds germinate in open sites which are relatively free of other vegetation, so that early interspecific interference is minimised. A single batch of yarrow seeds had at least five types of conditionally dormant seeds (Tables 2.1, 2.2, 2.3). While the availability of direct light was able to break the innate dormancy of all the viable yarrow seed, alternating temperature or presence of nitrate ions or cold temperature stratification or scarification was able to substitute for the light requirement in 30% to 50% of these seeds (Tables 2.1, 2.2, 2.3). The above environmental cues that promote the germination of yarrow seeds are more prevalent in open situations, at or near the soil surface (Thompson *et al.*, 1977; Hart, 1978). Therefore, the dormancy characteristics of the yarrow seeds are of strategic importance in that they help ensure that germination occurs in habits where the chances of successful seedling emergence and establishment are high.

Tillage of the land by conventional methods usually cultivates the soil to a plough depth of approximately 20 - 25 cm. The yarrow seeds lying on the soil surface can thus be buried at various depths ranging from the soil surface to 25 cm down the soil profile. When yarrow seeds were buried at 16 cm and 32 cm in the soil profile, approximately 50% and 60% of the seeds remained viable after 2 years, respectively (Fig. 2.3). However, during the same period of time the yarrow seeds

buried in the soil at depths of 8 cm or less lost their viability at a more rapid rate and less than 10% of seed was viable after a period of 2 years. The low and stable temperatures at the deeper soil depths and the increasingly low oxygen and high carbon dioxide levels down the soil profile have been suggested as possible reasons for the longer survival of seeds in the deeper layers of the soil (Turner, 1933; Bibbey, 1948). Conversely, the more favourable environment at the shallower depths in the soil may result in the germination of seeds *in situ* (Evans, 1960; Schafer and Chilcote, 1970) and this in turn would be responsible for the relatively short period of survival of seeds buried at these depths. Although a half life of over 2 years was observed for yarrow seed buried at 16 cm and 32 cm in undisturbed soil, it is not clear from the present study whether the survival rate of the seeds would be decreased in arable land which is regularly cultivated. However, it is likely that deep tillage leading to burial of seed favours the longevity of viability of yarrow seed, thus contributing to the persistance of this species on arable land. The viable buried seeds can give rise to seedling plants when they are subsequently returned to the open environment by further tillage and/or by other agencies such as earthworms and insects (Harper, 1977).

Except during the winter months most of the yarrow seeds lying on the soil surface germinated when adequate moisture was available (Fig. 2.1). The poor germination of seeds in the winter months was presumably due to the low temperature experienced at this time of the year (Appendix 1). In rainfed arable land in Canterbury, New Zealand, two main flushes of yarrow seed germination occurred, in spring and autumn (Appendix 15; Bourdot, 1980), when there was increased rainfall and the air temperature was sufficiently high for normal vegetative growth and development to occur (Appendix 1). In irrigated arable land, substantial germination of yarrow seeds was observed in spring, summer, and autumn (Kannangara,

unpublished). The germination of yarrow seeds in large numbers with the onset of favourable environmental conditions would undoubtedly increase the chance of at least a few of their seedlings establishing successfully.

Although the growth and development of seedling yarrow plants was markedly suppressed when the amount of light available to them decreased (Tables 3.1, 3.2 and 3.4; Bourdot, 1980), they were able to survive at light intensities as low as 6.4% of full daylight (Section 3.3.1). The similar densities of seedling yarrow present either in association with barley or pea crops or in a pure stand (Table 4.1) also indicated that yarrow plants had a great capacity to survive in the presence of interference for light (Appendix 7), mineral nutrients (Figs. 5.5, 5.6) and water (Section 4.4). Additionally, the seedling yarrow plants were also able to withstand the allelopathic effects of barley plants (see RYT in Fig. 5.5; Section 5.3). After the barley or pea crops were harvested in late summer, the surviving yarrow seedlings underwent rapid growth and development (Figs. 4.15, 4.17; Appendix 9c), undoubtedly as a result of the removal of direct inter-specific plant interference.

Seedling yarrow plants, established in pure stands in the spring, initiated rhizomes 8 weeks after emergence (Appendix 13) with the rhizome system undergoing rapid growth and development in the summer and autumn (Fig. 4.9, 4.17). Bourdot (1980) observed that there was a six-fold increase in the rhizome weight over the mild winter period experienced in the Canterbury Plains of New Zealand. Presumably as a consequence of apical dominance, most of the buds on the rhizomes attached to the parent plants remained in a quiescent state (Bourdot, 1980). This resulted in a substantial build-up of rhizome bud reserves in the soil (Bourdot, Field and White, 1982). They estimated that a pure stand of seedling yarrow establishing in early summer could produce approximately 24,000 rhizome buds m^{-2} by the following spring. When intact rhizomes were buried at 5 cm depth in the soil their buds remained viable for over 260

days and were able to produce new shoots when subsequently fragmented (Bourdot, 1982). However, all the buds on a rhizome fragment did not form shoots at the same time (Bourdot, 1980; Bourdot *et al.*, 1982). As the length of the rhizome fragments increased, a decreasing number of the buds present on them 'germinated', while the other buds remained quiescent until the shoots already growing on them were severed or destroyed and/or the rhizomes were further fragmented. The staggered 'germination' of the rhizome buds is likely to prevent the rapid loss of the bud reserves present in the soil and also increase the chance of the successful establishment of independent yarrow plants from them.

Overall characteristics of the seeds, the seedlings and the rhizomes of yarrow indicate that the species is well adapted to persist in field situations for a relatively long period of time.

Many workers have shown that certain morphological and physiological differences of plant species determine whether they are the aggressive or the suppressed species when grown in mixtures (Blaser *et al.*, 1956; Black, 1957, 1958, 1960; Harper, 1961; Donald, 1963; Idris and Milthorpe, 1966; Black *et al.*, 1969; Laskey and Wakefield, 1978; Haynes, 1980). A generalized list of some of the characteristics that determine the competitive ability (aggressivity) of weed species is as follows:

(i) The size and weight of seeds (i.e., the amount of embryonic capital in the seed).

(ii) Time of emergence.

(iii) Initial seedling vigour.

(iv) Net assimilation rate.

(v) Height, leaf area and leaf orientation.

(vi) Adaptability to changes in the light environment.

(vii) Development, growth and architecture of the root system.

(viii) Ability to fix atmospheric nitrogen.

(ix) Efficiency of water and mineral nutrient uptake and utilization.

(x) Drought resistance.

(xi) Allelopathic effects.

In the present study, although yarrow and barley or pea seedlings emerged from the soil at the same time (Sections 5.2.1.3, 5.2.3.3), the aggressivity of yarrow was low when grown in association with either of the latter two species (Table 5.1). Presumably, owing to the small size of the yarrow seed (Appendix 13), and its comparatively lower seed weight (Section 4.4), the yarrow seedlings were substantially smaller than the seedlings of barley and peas at the time of emergence from the soil. Additionally it was evident that the seedling vigour of yarrow was markedly less than that of the barley or pea seedlings (Fig. 4.1); the yarrow plants exhibited a prostrate, rosette-like growth habit compared to the taller and more spreading nature of the barley or pea plants and this resulted in the reduced light availability to yarrow in mixture with either of the latter two species (Appendix 7); the yarrow plants were relatively less efficient in the uptake of nitrogen, phosphorus and potassium than the barley or pea plants grown with them (Figs. 5.5, 5.6); and finally, allelopathic substances exuded by the barley plants appeared to suppress the growth of the neighbouring seedling yarrow plants (refer Section 5.3; RYT in Fig. 5.5). Therefore, it is not difficult to identify which factors were, at least partially, responsible for the low aggressivity of seedling yarrow when grown with barley or pea plants. There is no published evidence to suggest that other differences between seedling yarrow and barley or pea plants would have contributed to the low aggressivity of the former species.

The vegetative growth and development, including rhizome growth, of the seedling yarrow stand grown in association with the barley or pea

crop was markedly suppressed compared to its pure stand (Figs. 4.1, 4.3, 4.5, 4.7, 4.9), with barley being the more aggressive crop species. The greater penetration of light through the pea canopy (Appendix 7) and the absence of allelopathic effects by the pea plants (see RYT in Fig. 5.6) would have been partially responsible for the improved growth and development of seedling yarrow in the pea crop, while the ability of the nodulated pea plants (Section 4.2.6) to obtain symbiotically fixed nitrogen may have reduced their dependence on soil mineral nitrogen, and thereby making available a greater share of this nitrogen source for the growth and development of the associated yarrow plants. Furthermore, the ability of leguminous species to release symbiotically fixed nitrogen to the soil, especially during the latter stages of growth and development (Harper, 1964; Vallis, 1978), suggests that the pea plants may have supplied nitrogen to the associated yarrow seedlings. This may have been an additional factor responsible for the improved growth and development of seedling yarrow associated with the pea crop. Such factors may be also responsible for yarrow being a problemmatic weed in leguminous crops such as field peas and beans, and white clover seed crops (Bourdot *et al.*, 1979; Bourdot and Butler, 1981).

The barley crop suppressed the growth and development of seedling yarrow to the extent that the latter species did not adversely affect the seed yield of barley (Table 4.3). However, the markedly improved growth of the seedling yarrow stand in the pea crop had detrimental effects on the reproductive phase of the crop and resulted in a significant reduction in the pea seed yield (Table 4.3). Thus in addition to the highly specialized characteristics of yarrow which enable it to persist on arable land, it can also be an economically undesirable weed in a crop such as field peas, which affords relatively poor interference and may thus be classed as an opportunistic species.

From the present knowledge of the biology of yarrow it can be presumed that arable land infested with this species would have substantial seed and rhizome bud reserves in the soil. Owing to the poor aerodynamic efficiency of the yarrow seeds (Bostock, 1978), it is likely that the introduction of fresh seed from outside sources will be limited, while the spreading of the species via rhizome buds has been observed to be localized to an area close to the parent plants (Hilgendorf and Calder, 1952; Reynolds, 1961; Bourdot, 1980; Bourdot *et al.*, 1982). Thus if the seeds and rhizome buds already present in the soil can be exhausted while preventing fresh ones from forming, the yarrow can be effectively controlled on arable land. However, if such an approach of attrition is to be successful it is necessary to take into account all aspects of the plant's biology.

In the past, attempts to control yarrow on arable land were principally directed towards exhausting the rhizome bud reserves by repeated soil cultivation (Saxby, 1944; Hilgendorf and Calder, 1952). The chopping of rhizomes into approximately 4 cm pieces by shallow tillage of the soil followed by repeated severing of the newly emerging yarrow shoots before they formed new rhizomes enabled the total exhaustion of rhizome bud reserves within a period of 80 days (Bourdot, 1982). However, owing to the ability of the buried yarrow seed to remain viable for a long period of time (Fig. 2.3), it is doubtful whether the exhaustion of rhizome buds alone would lead to effective control of the species on arable land. Although fallowing of yarrow infested land for a relatively longer period may lead to its effective control, such an approach would not be acceptable to farmers as the land is unproductive for a long time. To overcome this problem, various combinations of mechanical and cultural practices were used by the farmers in the Canterbury Plains of New Zealand. However, many of these control measures have had only limited success. The lack of

knowledge of the biology of yarrow may have been a principal reason for the failure of these integrated measures to control the species. An alternative approach would be to use selective herbicides to control the yarrow growing in association with crops. However, at the present time no suitable selective herbicides are available for the post-emergence control of yarrow in crops such as field peas and beans and white clover seed crops (Field, personal communication).

In more recent times, the integration of certain mechanical and cultural practices may have unwittingly assisted in the control of yarrow. These practices include the burning of plant stubble on the land before tillage to kill any yarrow seed lying on the soil surface (refer Section 4.4); the minimum tillage of the soil to prevent unearthing yarrow seeds buried in the deeper layers in the soil profile (Fig. 2.3); set stocking of the land with sheep, immediately after minimum tillage, to remove surface lying and/or partially buried rhizomes; and rotational cropping the land for 2 to 3 years with cereal (e.g. barley) and winter green feed (e.g. kale (*Brassica oleracea*)) crops which effectively suppress the growth and development of yarrow. However, before effective integrated approaches to control yarrow can be positively formulated further studies are necessary to: (a) evaluate the long-term effects of minimum tillage on the growth and development of the crop species used in rotations; (b) identify other crop species which are as effective as barley in suppressing the growth and development of yarrow and could be used in arable cropping rotations; (c) evaluate different mechanical and/or cultural practices in relation to the time required for the exhaustion of the yarrow seeds and the rhizome buds from the soil; and (d) identify herbicides which selectively kill both seedlings and rhizomatous yarrow plants growing in association with crops.

APPENDIX 1: Climatic data* for the experimental periods in Chapters 2, 3, 4 and 5.

	1979										1980		
	M	A	M	J	J	A	S	O	N	D	J	F	M
Mean max. temp. (C)	18.6	17.6	13.0	12.0	11.7	10.3	14.9	15.6	19.0	21.9	22.4	21.0	18.2
Mean min. temp. (C)	11.0	5.5	3.9	1.1	2.0	2.2	4.5	6.0	8.7	9.9	10.6	10.7	9.9
Mean soil temp. (C)													
10 cm depth	14.9	10.8	7.5	4.9	4.6	4.9	7.9	11.0	14.3	16.8	16.8	16.5	13.7
20 cm depth	15.7	12.1	8.7	6.1	5.6	5.9	8.5	11.3	14.9	17.4	17.5	17.6	14.6
30 cm depth	16.2	12.9	9.6	6.7	6.3	6.6	9.1	11.7	15.2	17.7	17.9	18.1	15.3
Rainfall (mm) (total for month)	132.9	9.1	105.5	3.9	96.1	110.9	21.0	110.8	50.9	33.3	134.9	55.3	105.8
Solar radiation ($MJ\ m^{-2}\ month^{-1}$)								492.2	588.7	769.5	650.5	531.5	412.0

APPENDIX 1: (cont'd....)

	1980									1981		
	A	M	J	J	A	S	O	N	D	J	F	M
Mean max. temp. (C)	16.3	15.0	10.7	10.5	12.9	16.8	19.6	17.2	20.3	23.7	22.9	20.7
Mean min. temp. (C)	7.2	3.4	0.6	0.8	2.4	3.9	7.0	6.9	10.5	11.7	12.4	10.7
Mean earth temp. (C)												
10 cm depth	11.4	7.4	4.4	4.0	4.7	8.3	12.5	12.8	16.1	18.7	17.7	15.2
20 cm depth	12.4	8.9	5.6	4.9	5.7	8.9	12.4	13.4	16.6	19.3	18.7	15.9
30 cm depth	13.2	9.9	6.5	5.7	6.4	9.4	12.9	14.3	17.1	19.8	19.2	16.8
Rainfall (mm) (total for month)	46.6	8.3	79.3	39.9	47.8	1.1	12.7	85.4	28.7	25.4	12.0	41.2
Solar radiation ($MJ\ m^{-2}\ month^{-1}$)	245.6	204.8	135.1	159.1	272.0	415.6	579.9	633.5	652.8	696.1*	509.0	-

*1. Solar radiation was measured at Christchurch Airport (about 15 km from experimental sites).

2. All other measurements from Lincoln College Meteorological Station (about 0.5 km from experimental sites).

Appendix 2: Effect of green 'safe' light on the germination of yarrow seed after incubation at 25°C for 28 days (Chapter 2).

Treatment	Mean Germination (%)
Continuous dark	3.8
Continuous green 'safe' light	4.1
Continuous white light[#]	97.6
$L.S.D._{0.05}$	6.4
C.V. (%)	10.7

[#]From fluorescent + incandescent source (3875 Lux intensity).

APPENDIX 3: Effect of depth and duration of burial on the germination[#] of yarrow seed in the dark. Each value is a mean of four replicates. (Chapter 2 - Experiment 4).

Depths of burial (cm) \ Duration of burial (months)	3 (28.6.79)	6 (28.9.79)	9 (28.12.79)	12 (28.3.80)	15 (28.6.80)	18 (28.9.80)	21 (28.12.80)	24 (28.3.81)	$LSD_{0.05}$	C.V. (%)
0 (soil surface)	1.3	1.3	1.0	1.0	1.0	1.0	1.0	1.0	0.4	23.5
2	21.3	9.0	1.5	1.5	1.5	1.3	1.0	1.0	1.1	16.4
4	17.8	17.0	1.3	1.0	2.8	1.5	1.0	1.0	1.6	19.7
8	15.3	15.8	2.1	1.3	1.5	3.0	2.0	1.5	1.8	20.7
16	3.3	3.0	1.0	1.3	2.0	2.3	1.3	1.3	2.7	21.8
32	1.8	3.0	2.0	1.3	1.3	1.8	1.3	1.0	2.0	27.3
$L.S.D._{0.05}$	1.8	1.8	1.2	0.8	2.0	2.3	1.4	0.8		
C.V. (%)	12.0	14.6	34.5	44.7	32.6	16.8	14.3	10.9		

Germination tests were carried out by supplying 20-30°C diurnal alternating temperature.

APPENDIX 4: Effects of depth and duration of burial on germination[#] of yarrow seed (Chapter 2 - Experiment 4). Each value is a mean of four replicates.

Depths of burial (cm) \ Duration of burial (months)	3 (28.6.79)	6 (28.9.79)	9 (28.12.79)	12 (28.3.80)	15 (28.6.80)	18 (28.9.80)	21 (23.12.80)	24 (28.3.81)	$LSD_{0.05}$	C.V. (%)
0 (soil surface)	66.8	42.5	34.5	4.5	5.5	1.0	1.0	0.0	4.0	13.9
2	91.3	76.0	45.5	11.5	7.0	3.5	4.5	3.8	5.3	11.9
4	97.0	91.3	65.0	43.3	35.0	20.5	13.5	13.8	5.9	8.5
8	97.0	98.6	80.3	54.8	37.5	32.3	24.3	14.3	4.8	6.0
16	97.5	96.0	94.8	97.3	84.5	70.8	52.3	51.0	5.3	4.5
32	97.8	97.3	95.0	97.3	94.5	78.8	70.0	67.0	5.9	4.7
$L.S.D._{0.05}$	6.0	5.6	7.2	4.3	4.1	4.8	4.1	5.8		
C.V. (%)	4.5	4.5	7.9	5.6	6.3	9.3	9.9	15.5		

[#]Germination tests were carried out by supplying 20 - 30°C diurnal alternating temperature with 8 h light day^{-1} (I.S.T.A. recommendations, 1976); mean germination values are directly proportional to percentage viability of seed (refer text for details).

APPENDIX 5: Temperature recordings* within and outside the shade houses used in the shading experiment (Chapter 3). Values are daily maximums and minimums (C).

	Light Intensity (% Full Daylight)							
	100%		46.8%		23.7%		6.4%	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
7 February 1980	26.0	8.0	26.0	8.0	26.0	7.5	26.0	7.5
8 February 1980	25.0	6.0	25.0	5.0	24.5	4.5	24.0	4.5
9 February 1980	28.0	11.5	28.5	13.5	27.0	12.5	27.0	12.0
10 February 1980	24.0	6.0	24.0	6.0	23.5	5.5	23.0	5.0
11 February 1980	10.5	2.0	15.5	3.5	15.0	3.5	15.0	3.5
12 February 1980	18.5	2.5	18.5	3.0	18.5	3.0	19.0	3.0
13 February 1980	22.0	6.0	22.9	6.5	22.4	6.1	22.3	5.9
Mean	22.0	6.0	22.9	6.5	22.4	6.1	22.3	5.9
Mean difference between shade treatment and no shade			+0.9	+0.5	+0.4	+0.1	+0.3	-0.1

*The thermometer in each shade house was situated on a white wooden post, placed at the middle of the plot, and was 25 cm above ground level; it was oriented to the south.

APPENDIX 6: The relationship between seed number and seed weight* of yarrow. The highest and lowest weight is given in parenthesis.

Number Of Seed Lots	Number Of Seeds Per Lot	Mean Seed Weight Per 100 Seeds (mg)
200	100	16.1 (15.5 - 16.4)

*Seed dried to constant weight at 30°C.

APPENDIX 7: The percentages of the total available photosynthetically active radiation* (PAR) received at the surface of the yarrow populations in the crops and in pure stand. Each value is a mean of 5 measurements (Chapter 4).

Weeks After Seedling Emergence	Pure Stand	Yarrow in Barley	Yarrow in Peas
3	100	Not available	Not available
6	100	7	36
9	100	6	27
12	100	14	51
15	100	21	84

*PAR received by the yarrow populations in association with the crops were measured between two crop rows in their appropriate stands.

APPENDIX 8: Plant growth analysis - an outline of the basic concepts involved, 'classical' and 'functional' approaches, and the clarification of the statistical procedures used in the current studies (Chapter 4).

(i) Basic Concepts of Growth Analysis

Many workers have explained in detail the basic concepts of plant growth analysis and their physiological implications (e.g., Gregory, 1917; Blackman, 1919; Heath and Gregory, 1938; Watson, 1952; Whitehead and Myerscough, 1962). Measurements of total dry plant material present (a) in whole plant, (b) above ground level, or (c) as some distinctive plant fraction (e.g., root, stem or leaf) and the magnitude of the assimilatory system of that plant material as (a) leaf area, (b) total photosynthetic area, (c) leaf protein, (d) leaf chlorophyll, etc. (Watson, 1952; Williams, 1946) over time are required to carry out a growth analysis. The above measurements can be expressed as a 'per plot' or 'per unit area of crop' basis. The concepts of growth analysis can be applied to these measurements regardless of the basis on which they are expressed (Hunt, 1978).

In the study of the quantitative changes occurring when seedling yarrow plants interfere with either the barley or pea crops, growth analysis was carried out on the relevant measurements and expressed on a 'per unit area of crop' (Chapter 4). This was because the use of the other concepts which are designed exclusively for the study of the growth of plant populations (Watson, 1952) does not enable the evaluation of the changes in the specific leaf areas and leaf weight ratios of the different yarrow stands and the effects of these changes on their leaf area ratios.

The general formulae for the attributes of growth of populations studied in Chapter 4 are:

growth rates of leaf area

$$LA = dLA/_{dt}$$

growth rate of leaf weight

$$LW = dLW/_{dt}$$

growth rate of stem weight

$$SW = dSW/_{dt}$$

growth rate of rhizome weight

$$R_zW = dR_zW/_{dt}$$

total growth rate

$$W = dW/_{dt} ,$$

where 't' is the time period of growth and 'LA', 'LW', 'SW', 'R_zW', and 'W' are the leaf area, leaf weight, stem weight, rhizome weight and total plant weight, respectively. The other attributes studied included:

relative growth rate (RGR)

$$RGR_x = \frac{1}{x} \cdot \frac{dx}{dt} \quad , \quad \text{where 'x' can be LA, LW, SW, } R_zW \text{ or W.}$$

leaf area ratio (LAR)

$$LAR = LA/_W$$

specific leaf area (SLA)

$$SLA = \frac{LA}{LW}$$

leaf weight ratio (LWR)

$$LWR = \frac{LW}{W}$$

net assimilation rate

$$NAR = \frac{1}{LA} \cdot \frac{dW}{dt} \quad ; \text{ the letter symbols are as described above.}$$

The SLA and LWR are inter-related as:

$$\frac{LA}{W} = \frac{LA}{LW} \times \frac{LW}{W}$$ (Radford, 1967). At any instant of time, RGR, LAR and NAR are inter-related as:

$$\frac{1}{W} \cdot \frac{dW}{dt} = \frac{LA}{W} \times \frac{1}{LA} \cdot \frac{dW}{dt}$$ (Briggs, Kidd and West, 1920).

(ii) 'Classical' and 'Functional' Approach to Growth Analysis

In the 'classical' approach to growth analysis, the mean values of the various plant attributes, described above, are calculated over a given time interval (Radford, 1967). There are many limitations in this approach (Hughes and Freeman, 1967); the necessity to make assumptions regarding the complex physiological relationships between LA and W, which may deviate from the assumed linear relationship owing to the ontogenetic drifts of the population and the effects of the changing ambient conditions, has been indicated as one of the major drawbacks of the 'classical' approach to growth analysis (Radford, 1967).

To overcome the major limitations in the 'classical' method of growth analysis, the 'functional' approach, which uses regression procedures, was evolved; Kvet *et al.* (1971) provides a complete description of this method. The principle of this method consists of choosing a suitable mathematical function, represented by a smooth curve, which best fits the recorded LA or dry weight values of LW, SW, $R_z W$ or W; the fitted curve then approximates the real growth curve. Fitted values of data are extracted from the smooth curve and used to calculate instantaneous values of other growth attributes described earlier (e.g., RGR, LAR, SLA, LWR, NAR, etc.). Their time course can be followed by plotting these derived values against time.

The regression equations derived for LA, LW, SW, $R_z W$ and W can be linear, quadratic, cubic or of a higher order. In their generalized form, they can be represented as:

$$\text{Log}_e \text{ LA} = a_1 + b_1 t^1 + \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots n_1 t^v$$

$$\text{Log}_e \text{ LW} = a_2 + b_2 t^1 + \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots n_2 t^w$$

$$\text{Log}_e\ SW = a_3 + b_3t^1 + \ldots\ldots\ldots\ldots\ldots\ldots\ n_3t^x$$

$$\text{Log}_e\ R_zW = a_4 + b_4t^1 + \ldots\ldots\ldots\ldots\ldots\ldots\ n_4t^y$$

$$\text{Log}_e\ W = a_5 + b_5t^1 + \ldots\ldots\ldots\ldots\ldots\ldots\ n_5t^z$$

The RGR of these plant attributes are derived by differentiation of the appropriate equation -

$$RGR_A = \frac{1}{LA} \cdot \frac{dLA}{dt} = \frac{d\ (\text{Log}_e\ LA)}{dt}$$

$$RGR_{LW} = \frac{1}{LW} \cdot \frac{dLW}{dt} = \frac{d\ (\text{Log}_e\ LW)}{dt}$$

$$RGR_{SW} = \frac{1}{SW} \cdot \frac{dSW}{dt} = \frac{d\ (\text{Log}_e\ SW)}{dt}$$

$$RGR_{R_zW} = \frac{1}{R_zW} \cdot \frac{dR_zW}{dt} = \frac{d\ (\text{Log}_e\ R_zW)}{dt}$$

$$RGR_W = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{d\ (\text{Log}_e\ W)}{dt}$$

The various ratios were derived as follows:

$$LAR = \frac{LA}{W} = \text{antilog}\ (\text{Log}_e\ LA - \text{Log}_e W)$$

$$SLA = \frac{LA}{LW} = \text{antilog}\ (\text{Log}_e\ LA - \text{Log}_e LW)$$

$$LWR = \frac{LW}{W} = \text{antilog}\ (\text{Log}_e\ LW - \text{Log}_e W)$$

The NAR was obtained by:

$$NAR = \frac{RGR_W}{LAR} = \frac{d(Log_e W)}{dt} \div \text{antilog } (Log_e LA - Log_e W)$$

(iii) Statistical Procedures Used in Plant Growth Analysis (Chapter 4)

The details of the statistical procedures followed are given in the Algol computer programme written by Hughes and Freeman (1967). Bourdôt (1980) re-wrote the programme in Fortran and modified it to enable the fitting of polynomials of a higher order than cubics and the calculation of the variance of derived ratios and NAR when polynomials of different orders were fitted to W and LA. It is this modified programme that was used for the analysis of the data in Chapter 4.

Before the above computer programme was used, an analysis of variance of the orthogonal regression components was carried out on the relevant raw dry weight and leaf area data of the seedling yarrow and crops. In yarrow, the data subjected to this analysis were LW, SW, $R_z W$, W and LA (Appendices 9A, 9C), while in the barley and pea crops their respective W and LA were analysed (Appendix 9B). The best fit regression was chosen depending on the highest component declared significant for the time component. For example, in Appendix 9A, a cubic function was fitted to $\log_e$ yarrow leaf area factor.

(a) Curve fitting: A generalization of the statistical procedures followed in the calculation of the variance of the different growth analysis ratios and NAR when $\log_e A$ and $\log_e W$ were described by a quadratic and cubic function, respectively, as in Appendix 9B (barley crop in association with yarrow) is given below:

Fitted cubic equation to $\log_e W$:

$$Log_e W = a + bt + ct^2 + dt^3 + e \qquad (1)$$

$$= -1.776 + 2.89531\ t - 0.3371111\ t^2 + 0.013095679\ t^3$$

where the terms a, b, c, and d represent the 'true' curve and e the error of observations. The errors are assumed to be independent and normally distributed with zero mean and same variance; they usually cancel out.

It is convenient to present equation (1) as follows:

$$\text{Log}_e W = a_1 + b_1\ (\text{Lin}) + C_1\ (\text{quad}) + d_1\ (\text{cub}) + e \qquad (2)$$

where

Const = 1

Lin = t + A

quad = t^2 + Bt + C

cub = t^3 + Dt^2 + Et + F

Const = 1

Lin = t - 7.50

quad = t^2 - 15.00 t + 45.00

cub = t^3 - 22.50 t^2 + 150.30 t - 283.50

and

$$A = -\frac{\Sigma[(\text{Const})\ t]}{\Sigma(\text{Const})} = -7.50$$

$$B = -\frac{\Sigma(\text{Lin})\ t^2}{\Sigma(\text{Lin})\ t} = -15.00$$

$$C = -\frac{\Sigma[(\text{Const})t^2] + B\ \Sigma[(\text{Const})\ t]}{\Sigma(\text{Const})} = 45.00$$

$$D = -\frac{\Sigma(\text{quad})\ t^3}{\Sigma(\text{quad})\ t^2} = -22.50$$

$$E = -\frac{\Sigma[(\text{Lin})\ t^3] + D\ \Sigma[(\text{Lin})\ t^2]}{\Sigma[(\text{Lin})\ t]} = 150.30$$

$$F = -\frac{\Sigma(\text{Const})\ t^3 + D\ \Sigma(\text{Const})\ t^2 + E\ \Sigma(\text{Const})\ t}{\Sigma(\text{Const})} = -283.50$$

The coefficients a_1, b_1, c_1 and d_1 are estimated by the 'least squares' method:

		Variance
$\hat{a}_1$	$= \frac{1}{n} \Sigma (\log_e W)$	$\frac{\sigma^2}{n}$
$\hat{b}_1$	$= \frac{\Sigma (lin)\ (\log_e W)}{\Sigma\ (Lin)^2}$	$\frac{\sigma^2}{\Sigma (lin)^2}$
$\hat{c}_1$	$= \frac{\Sigma (quad)\ (\log_e W)}{\Sigma (quad)^2}$	$\frac{\sigma^2}{\Sigma (quad)^2}$
$\hat{d}_1$	$= \frac{\Sigma (cub)\ (\log_e W)}{\Sigma (cub)^2}$	$\frac{\sigma^2}{\Sigma (cub)^2}$

N.B. Summation is carried out over all data values; in this example, (n = 4 harvests x 6 replicates = 24).

By excluding the (cub) and $\hat{d}_1$ calculation and using the same procedure as above, a quadratic equation was fitted to $\log_e LA$:

$$\log_e LA = a + bt + ct^2 + e$$

$$= 7.558 + 0.93752\ t - 0.0770806\ t^2 + e \qquad (3)$$

The error variance for $\log_e W$:

$$\sigma^2_{\log_e W} = \frac{\text{error SS}}{\text{error d.f}} = \frac{7.66}{15} = 0.5107$$

The error variance for $\log_e LA$ ($\sigma^2_{\log_e LA}$), where a quadratic function was fitted, is estimated by adding the sums of square of cubic component into the error sums of square (error SS) and dividing by the revised degrees of freedom (d.f.):

$$\sigma^2_{\log_e LA} = \frac{2.41 + 24.49}{16} = 1.6813$$

The $\sigma^2_{\log_e W}$ of a fitted value in equation (2) is calculated by:

$$\sigma^2_{\log_e W} \left[\frac{1}{n} + \frac{(lin)^2}{\Sigma(lin)^2} + \frac{(quad)^2}{\Sigma(quad)^2} + \frac{(cub)^2}{\Sigma(cub)^2} \right] \qquad (4)$$

The square root of (4) gives the standard error of the fitted value of $\log_e W$.

Similarly for equation (3):

$$\sigma^2_{\log_e LA} \left[\frac{1}{n} + \frac{(lin)^2}{\Sigma(lin)^2} + \frac{(quad)^2}{\Sigma(quad)^2} \right] \qquad (5)$$

The square root of (5) gives the standard error of the fitted $\log_e LA$ value.

The confidence limit of the fitted value is calculated by multiplying the standard error of the fitted value by the two tailed 95% probability Students t value ($t_{15(0.05)}$ for $\log_e W$ and $t_{16(0.05)}$ for $\log_e LA$).

(b) Derived functions from the fitted curves:

$$RGR_X = \frac{1}{X} \cdot \frac{dX}{dt} = \frac{d(\log_e X)}{dt}$$

where 'X' can be LA, LW, SW, $R_z W$ or W

$$= \frac{d\left[a_1 + b_1(\text{lin}) + c_1\ (\text{quad}) + d_1\ (\text{cub})\right]}{dt}$$

$$= b_1 + c_1\ (2\ t + B) + d_1\ (3\ t^2 + 2\ Dt + E)$$

variance of a fitted RGR value:

$$\sigma^2_{\log_e W}\left[\frac{1}{\Sigma(\text{lin})^2} + \frac{(2\ t + B)^2}{\Sigma(\text{quad})^2} + \frac{(3\ t^2 + 2\ Dt + E)^2}{\Sigma(\text{cub})^2}\right] \qquad (6)$$

Square root of (6) gives standard error; the confidence limit of fitted RGR value is obtained in a similar way as described above.

$$\text{LAR} = \frac{\text{LA}}{W} = \text{antilog}\ (\log_e \text{LA} - \log_e W).$$

Variance of a fitted LAR value when quadratic and cubic functions have been fitted to $\log_e$LA and $\log_e$W respectively, are calculated as follows:

$$\sigma^2_{\log_e W}\left[\frac{1}{n} + \frac{(\text{lin})^2}{\Sigma(\text{lin})^2} + \frac{(\text{quad})^2}{\Sigma(\text{quad})^2} + \frac{(\text{cub})^2}{\Sigma(\text{cub})^2}\right]$$

$$+ (\sigma^2_{\log_e \text{LA}} - 2\ c)\left[\frac{1}{n} + \frac{(\text{lin})^2}{\Sigma(\text{lin})^2} + \frac{(\text{quad})^2}{\Sigma(\text{quad})^2}\right]$$

The 'c' in the above expression represents the covariance of the data of $\log_e$W and $\log_e$LA:

$$\hat{c} = \frac{\text{residual sum of products in ANOVA\#}}{\text{error degrees of freedom}}$$

\#Analysis of variance

The LWR and SLA are obtained in a similar way.

$$NAR = \frac{1}{LA} \cdot \frac{dW}{dt} = \frac{RGR}{LAR} = \frac{1}{W} \cdot \frac{dW}{dt} \div \frac{LA}{W}$$

Variance of a fitted NAR value when quadratic and cubic functions are fitted to $\log_e LA$ and $\log_e W$:

$$\left[\frac{\sigma^2 \text{ (fitted RGR)}}{(\text{fitted LAR})^2}\right] + \left[(\text{fitted RGR})^2 \times \sigma^2 \text{ (fitted LAR)}\right]$$

$$- \left[2 \frac{\text{fitted RGR}}{\text{fitted LAR}} \times \text{Cov (fitted RGR, fitted LAR)}\right.$$

where

$$\text{Cov (fitted RGR, fitted LAR)}$$

$$= \sigma^2_{\log_e W} \text{ (fitted LAR)} \left(\frac{\text{lin}}{\Sigma(\text{lin})^2} + \frac{\text{quad}(2t + B)}{\Sigma(\text{quad})^2}\right)$$

$$= \sigma^2_{\log_e W} \text{ (fitted LAR)} \left[\frac{\text{lin}}{\Sigma(\text{lin})^2} + \frac{\text{quad}(2\ t + B)}{\Sigma(\text{quad})^2} + \frac{\text{cub}\ (3\ t^2 + 2\ Dt + E)}{\Sigma(\text{cub})^2}\right]$$

$$+ c \text{ (fitted LAR)} \left[\frac{\text{lin}}{\Sigma(\text{lin})^2} + \frac{\text{quad}\ (2t + B)}{\Sigma(\text{quad})^2}\right]$$

Standard errors and confidence intervals are calculated as described previously.

APPENDIX 9A: Partitioned time sums of squares (obtained by ANOVA[√] of the appropriate raw data of seedling yarrow) by the use of orthogonal polynomials.[#] The time scale of the experiments was from 3 to 15 weeks after seedling emergence.

Source	d.f.	$Log_e LW$	$Log_e SW$	$Log_e W$	$Log_e LA$
(i) Yarrow/Barley Experiment					
Time	4	998.83*	488.18*	716.39*	348.48*
Linear	1	837.59*	449.17*	636.84*	331.92*
Quadratic	1	143.41*	22.98*	66.83*	1.16 ns.
Cubic	1	14.04*	12.84*	11.47*	10.65*
Quartic	1	(3.79) ns	(2.19) ns	(1.25) ns	(4.75) ns
Error	50	235.50	225.47	183.60	194.91
(ii) Yarrow/Pea Experiment					
Time	4	1391.82*	681.10*	980.11*	484.29*
Linear	1	1231.71*	648.90*	908.13*	464.11*
Quadratic	1	135.41*	15.67*	56.14*	9.72*
Cubic	1	22.83*	16.47*	14.39*	10.32*
Quartic	1	(1.87) ns	(0.06) ns	(1.45) ns	(0.14) ns
Error	50	120.87	171.80	123.02	132.18
		$Log_e R_z W$			
(iii) Yarrow in Pure Stand					
Time	2	58.26*			
Linear	1	57.35*			
Quadratic	1	(0.91) ns			
Error	10	12.38			

[#]The details of the method of partitioning are given in Steel and Torrie (1960), Chapter 11

(a) Probability (95%) was tested against error variance with the appropriate degree of freedom:
* = significant; ns = not significant.

(b) Values which were subsequently pooled with the error term are given in parenthesis.

(c) Each experiment was replicated 6 times.

[√]Analysis of variance.

APPENDIX 9B: Partitioning of the time sums of squares (obtained by the ANOVA[√] of the appropriate raw data of the crops) by the use of orthogonal polynomials.[#] Time scale of the experiments was from 3 to 12 weeks after seedling emergence.

Source	d.f.	$Log_e W$	$Log_e LA$
(i) Barley in Association with Yarrow			
Time	3	75.10*	50.15*
Linear	1	60.01*	19.88*
Quadratic	1	12.91*	27.86*
Cubic	1	2.18 *	(2.41) ns
Error	15	7.66	24.49
(ii) Peas in Association with Yarrow			
Time	3	145.67*	52.19*
Linear	1	133.44*	32.82*
Quadratic	1	11.50*	18.49*
Cubic	1	(0.73) ns	(0.88) ns
Error	15	7.08	7.38

[#]The details of the method of partitioning are given in Steel and Torrie (1960), Chapter 11
(a) Probability (95%) was tested against error variance with the appropriate degree of freedom: * = significant; ns = not significant.
(b) Values which were subsequently pooled with the error term are given in parenthesis.
(c) Each experiment was replicated 6 times.

[√]Analysis of variance.

APPENDIX 9C: Partitioned time sums of squares (obtained by ANOVA[√] of the appropriate raw data of yarrow) by the use of orthogonal polynomials.[#] Time scale of the experiments was from 15 to 33 weeks after seedling emergence (i.e., up to 18 weeks after the crops were harvested).

Source	d.f.	$Log_e LW$	$Log_e R_z W$	$Log_e W$	$Log_e LA$
(i) Yarrow/Barley Experiment					
Time	3	57.23*	275.71*	46.01*	28.28*
Linear	1	6.77*	220.39*	25.24*	2.13 ns
Quadratic	1	49.47*	44.02*	14.25*	18.06*
Cubic	1	(0.99) ns	11.30*	6.51*	9.09*
Error	39	83.67	144.14	79.90	103.77
(ii) Yarrow/Pea Experiment					
Time	3	38.15*	152.60*	21.92*	52.47*
Linear	1	13.79*	111.65*	4.20*	20.11*
Quadratic	1	21.73*	27.06*	12.15*	27.68*
Cubic	1	(2.63) ns	13.88*	5.56*	4.68*
Error	39	45.75	93.25	35.36	44.88

[#]Same as in Appendix 9A.

[√]Analysis of variance

APPENDIX 10: The observed means m^{-2} of the natural logarithms* of LA, LW, SW, $R_z W$ and W of yarrow at different times after seedling emergence (Chapter 4).

	Weeks After Seedling Emergence				
	3	6	9	12	15
Leaf Area (LA)					
Yarrow in pure stand	4.0	6.3	9.8	10.6	10.7
Yarrow in pea crop	4.1	5.4	6.1	7.4	8.7
Yarrow in barley crop	4.0	3.4	3.9	4.4	6.7
Leaf Weight (LW)					
Yarrow in pure stand	-4.8	1.3	4.9	5.8	6.2
Yarrow in pea crop	-4.8	-0.6	1.6	1.8	6.0
Yarrow in barley crop	-4.8	-1.8	-0.5	-1.0	1.5
Stem Weight (SW)					
Yarrow in pure stand	-2.2	0.2	3.1	4.7	5.6
Yarrow in pea crop	-3.1	0.2	0.7	0.4	2.5
Yarrow in barley crop	-3.3	-2.1	-1.4	-1.2	-0.9
Rhizome Weight ($R_z W$)					
Yarrow in pure stand	0	0	1.1	2.7	3.8
Yarrow in pea crop	0	0	0	0	2.3
Yarrow in barley crop	0	0	0	0	-4.6
Total Weight (W)					
Yarrow in pure stand	-2.1	2.2	5.1	6.2	6.7
Yarrow in pea crop	-2.9	0.7	2.0	2.1	6.1
Yarrow in barley crop	-3.0	-1.2	0.7	-0.4	1.7

*The original values for LA were in cm^2 m^{-2} and for LW, SW, $R_z W$ and W in g m^{-2}.

APPENDIX 11: The observed means m^{-2} of the natural logarithms* of LA and W of the barley and pea crops at different times after seedling emergence (Chapter 4).

	Weeks After Seedling Emergence			
	3	6	9	12
Leaf Area (LA)				
Pure stand of peas	8.3	9.3	10.3	9.9
Pea crop with yarrow	8.3	9.8	10.5	9.8
Pure stand of barley	9.5	10.5	9.7	8.4
Barley with yarrow	9.6	10.7	9.4	7.8
Total Weight (W)				
Pure stand of peas	3.1	4.7	6.2	6.6
Pea crop with yarrow	3.2	5.0	6.4	6.5
Pure stand of barley	4.2	6.1	6.4	6.9
Barley with yarrow	4.2	6.3	6.5	7.1

*The original values for LA were in cm^2 m^{-2} and for W in g m^{-2}.

APPENDIX 12: The observed means m^{-2} of the natural logarithms* of LA, LW, SW, R_zW, and W of yarrow after the barley and pea crops were harvested. The number of weeks from crop harvest are in parenthesis (Chapter 4).

	Weeks After Seedling Emergence			
	15 (0)	21 (6)	27 (12)	33 (18)
Leaf Area (LA)				
Yarrow in pure stand	10.7	10.8	9.3	8.0
Yarrow previously in pea crop	8.7	10.6	9.6	8.6
Yarrow previously in barley crop	6.7	8.6	7.9	7.9
Leaf Weight (LW)				
Yarrow in pure stand	6.1	6.7	5.1	3.7
Yarrow previously in pea crop	2.3	5.4	5.9	5.7
Yarrow previously in barley crop	1.5	3.8	3.3	1.6
Stem Weight (SW)				
Yarrow in pure stand	6.0	7.1	6.0	4.8
Yarrow previously in pea crop	4.4	5.5	4.1	4.2
Yarrow previously in barley crop	-0.8	-0.1	2.2	3.4
Rhizome Weight (R_zW)				
Yarrow in pure stand	3.8	6.3	5.7	5.7
Yarrow previously in pea crop	2.3	5.4	4.9	5.7
Yarrow previously in barley crop	-4.6	2.2	1.4	3.3
Total Weight (W)				
Yarrow in pure stand	6.7	7.9	6.3	6.3
Yarrow previously in pea crop	6.1	6.9	5.8	6.1
Yarrow previously in barley crop	1.7	4.0	3.7	4.4

*The original values for LA were in cm^2 m^{-2} and for LW, SW, R_zW and W in g m^{-2}.

APPENDIX 13: Vegetative development and sexual reproduction in spring-germinating seedling yarrow (Chapter 4).

Yarrow is an important weed in the arable lands of the Canterbury Plains in New Zealand (Bourdôt, White and Field, 1979). It has the ability to propagate by vegetative and sexual means, and is known to produce large quantities of rhizomes and seeds which are a potential source of infestation of farming lands. The seedling plants that emerge after spring cultivation grow in association with crops and often become a problem weed in white clover (*Trifolium repens*) seed crops, pea (*Pisum sativum*), beet (*Beta vulgaris*) and bean (*Phaseolus vulgaris*) crops (Kannangara, unpublished).

It is evident from the recent literature review on yarrow (Bourdôt, 1980) that the information on the biology of seedling plants is sparse. The life history studies of yarrow seedlings, conducted by Bourdôt (1980), were carried out on individual plants growing in undisturbed and interference-free environment. However, a population of seedling yarrow growing on an arable land may show marked variation in their development. The present observations were carried out to obtain a better understanding of the vegetative development and sexual reproduction of a spring-emerging seedling yarrow population growing on arable land.

The experimental site and design (Section 4.2.1), soil sterilization method (Section 4.2.2), seedling density of yarrow (Section 4.2.3), yarrow seed used (Section 4.2.4), and the establishment of the pure yarrow stand (Section 4.2.5) are detailed in Chapter 4. The sampling procedure, measurements, and observations made are as follows.

Taking 5 October 1979 as the time of seedling emergence, weekly samples were taken over a period of 21 weeks. Plants within a randomly selected quadrat area of 0.12 m^2 were removed from each replicate at each sampling, care being taken to ensure that the least possible damage occurred to the subterranean parts of the plants. The soil was carefully washed from the subterranean parts of the plants. The plants from the 6 replicates were bulked together. During the first 7 samplings, the plants were separated into different lots, based on their visual size; at the following 6 samplings the plants were categorized on the presence or absence of rhizomes. From the 14 to 21 sampling, the presence or absence of flowering stems was the criterion for grouping the plants.

At each sampling, the group with the highest number of yarrow plants was taken to be representative of its development stage, and a few of these plants were photographed to record their developmental stage (Plates 2 - 9).

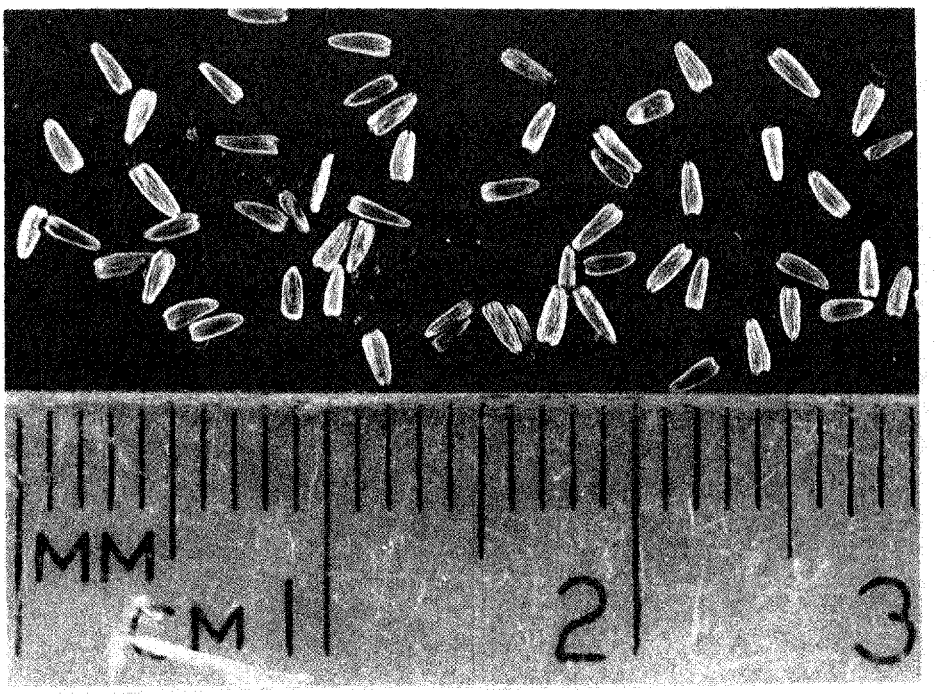


Plate 1: Yarrow Seeds*

*Dry indehiscent fruit more correctly referred to as an achene.

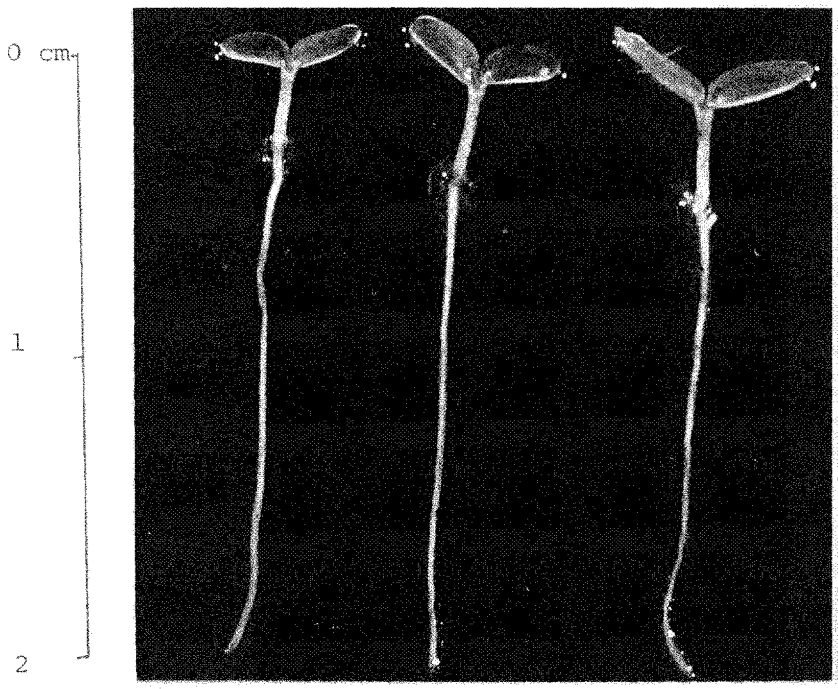


Plate 2: Seedling yarrow plants - one week after emergence. Note expanded cotyledons and tap root.

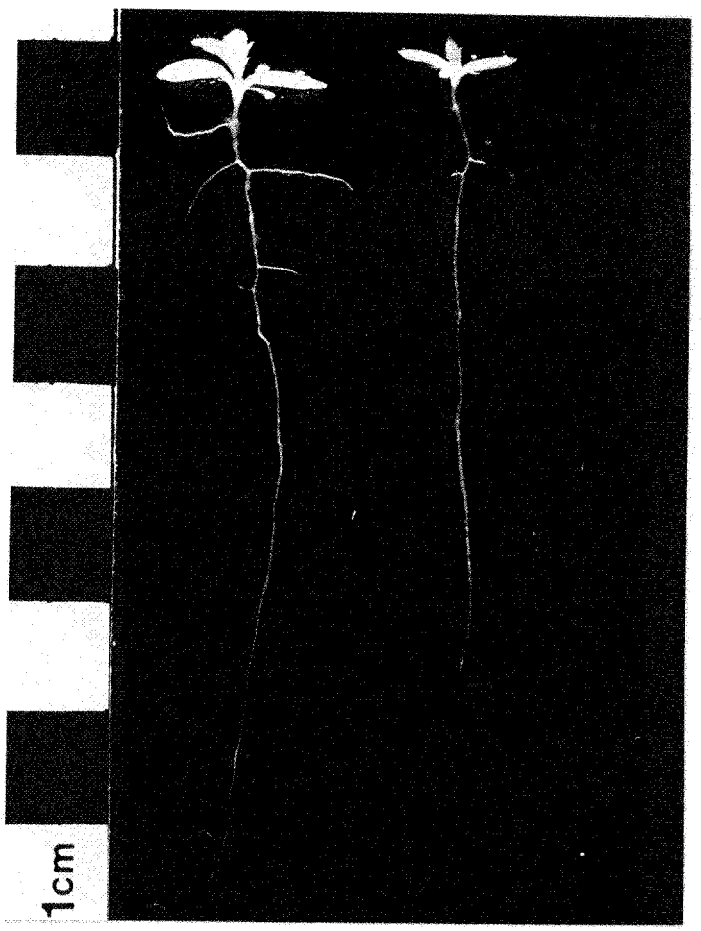


Plate 3: Seedling yarrow plants - two weeks after emergence. Note the presence of first pair of true leaves and primary root$ developing from the tap root.

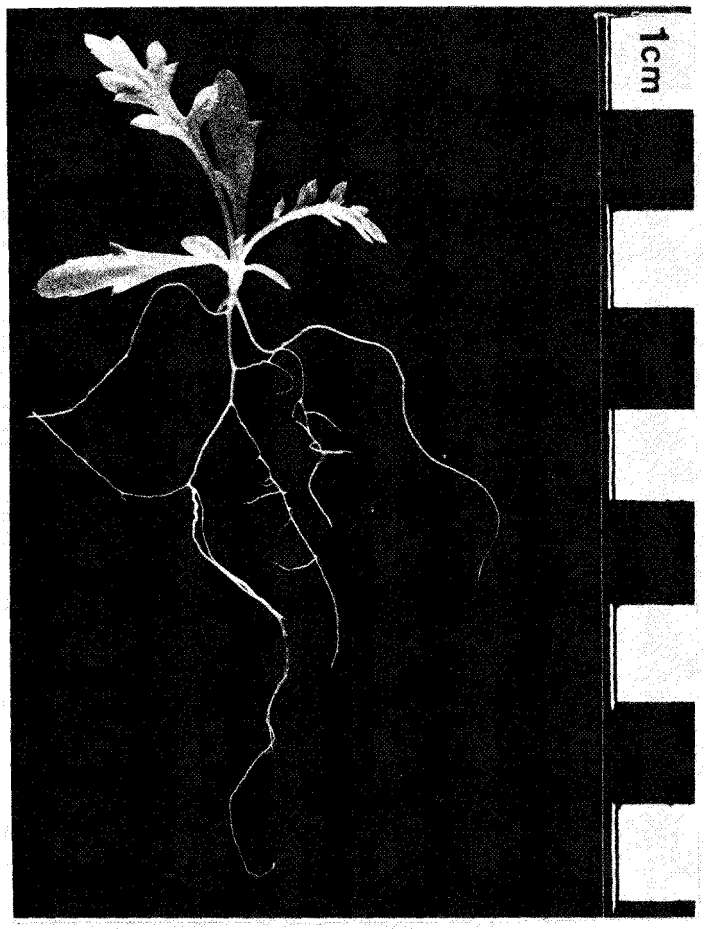


Plate 4: Seedling yarrow plant - four weeks after emergence. Note the presence of four true leaves, persistence of cotyledons and secondary root development.

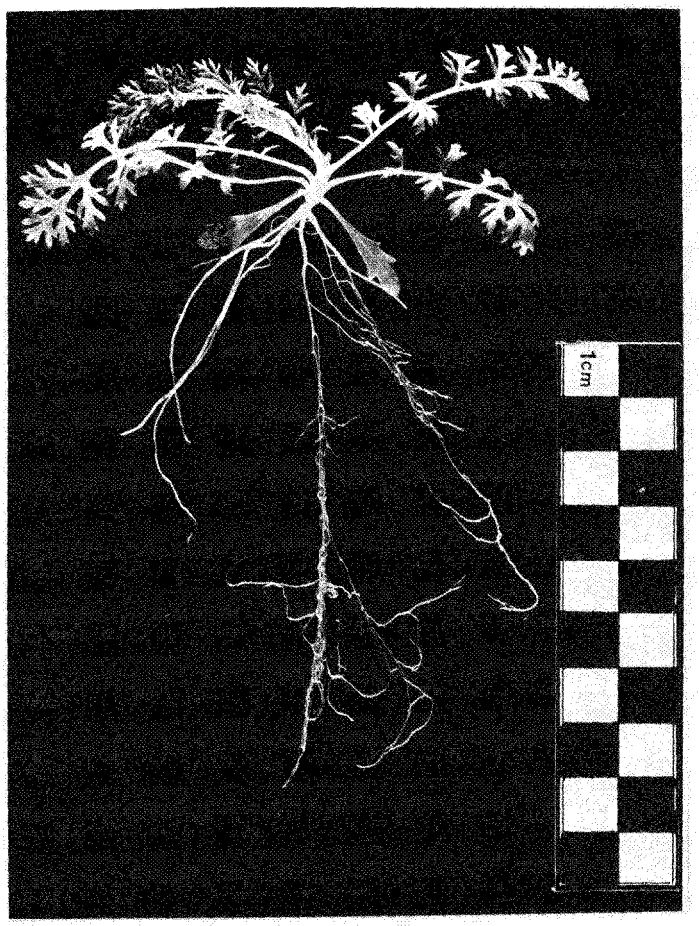


Plate 5: Seedling yarrow plant - six weeks after emergence. Eight true leaves are present and the cotyledons have abscised.

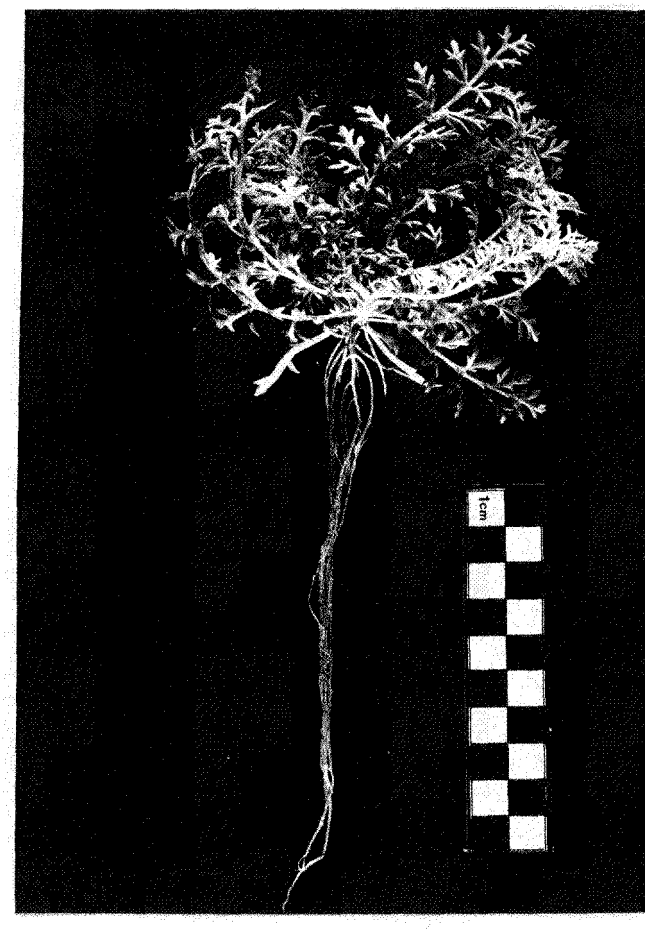


Plate 6: Seedling yarrow plant - eight weeks after emergence. Fourteen true leaves present and rhizomes have initiated.

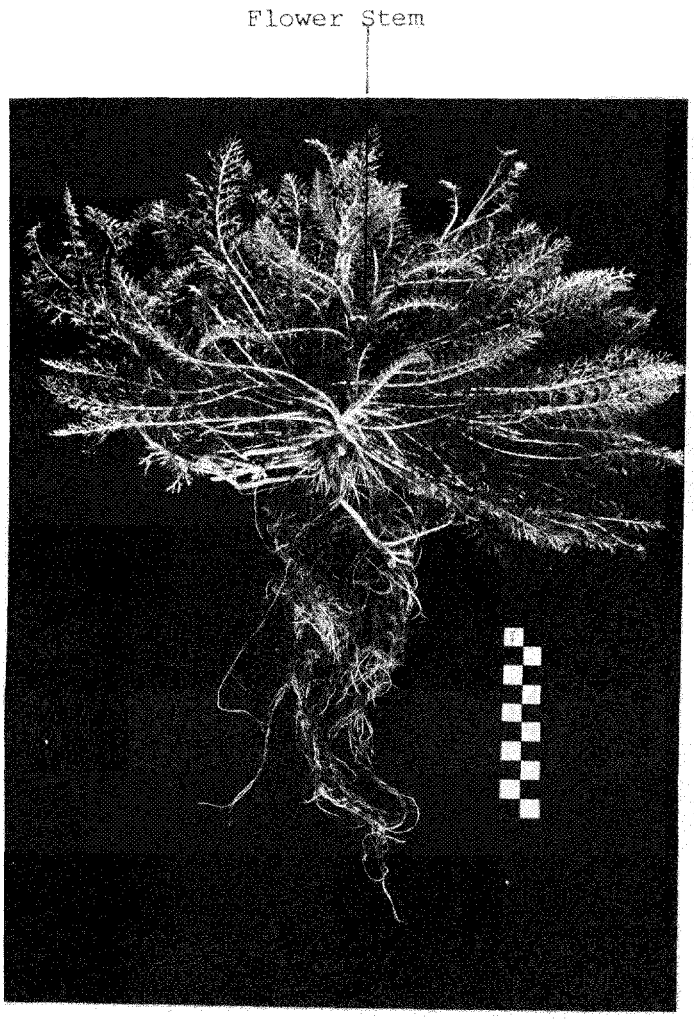


Plate 7: Seedling yarrow plant - thirteen weeks after emergence. Flower stem elongation has commenced and a few apical buds of the rhizome system have started leaf production.

Plate 8: General view of seedling yarrow plants fourteen weeks after emergence. Note the elongating flowering stems.

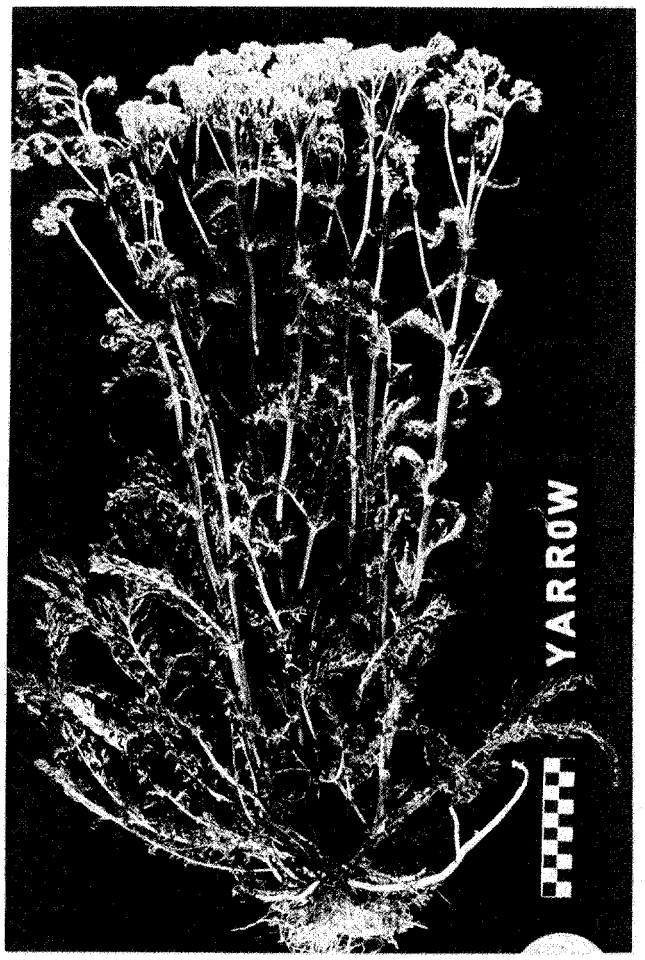


Plate 9: Seedling yarrow plant twenty weeks after emergence. Note the highly branched flowering stem and the arrangement of the capitula in corymbs.

N.B.: Each division of the scale (black or white) represents 1 cm.

On 15 February 1980, when the first formed inflorescences were dehydrating, the number of flowering stems and capitula in a quadrant area of 0.24 m^2 was recorded in each replicate. Two hundred mature capitula, from which no obvious seed shedding had occurred, were randomly selected from each replicate and carefully dissected to determine the number of seed $capitulum^{-1}$. The product of the mean seed number $capitulum^{-1}$ and total number of capitula gave an estimate of total seed production per unit area. The above measurements are summarized in Appendix 14.

After 21 weeks from seedling emergence, further visual observations were made, until 14 September 1980, to determine the time period of seed shedding, germination of shed seed, and fate of the parent plant. The observations and measurements made on spring-emerging seedling yarrow plants together with other information collected throughout the study period, were used to compile the life history diagram presented in Appendix 15.

APPENDIX 14: Components of seed yield in a population* of spring-emerging seedling yarrow. Each value is a mean of six replicates. (The maximum and minimum values are given in parenthesis.)

Flowering Stems m^{-2}	Capitula m^{-2}	Seed Capitulum^{-1}	Seed# Weight (mg)	Estimated Seeds m^{-2}
127.0	12,319.0	19.7	0.158	242,684
(124.0 - 131.0)	(10,788.0 - 16,330.0)	(16 - 25)	(0.156 - 0.162)	(72,608 - 408,270)

*Mean population size - 57.5 plants m^{-2}

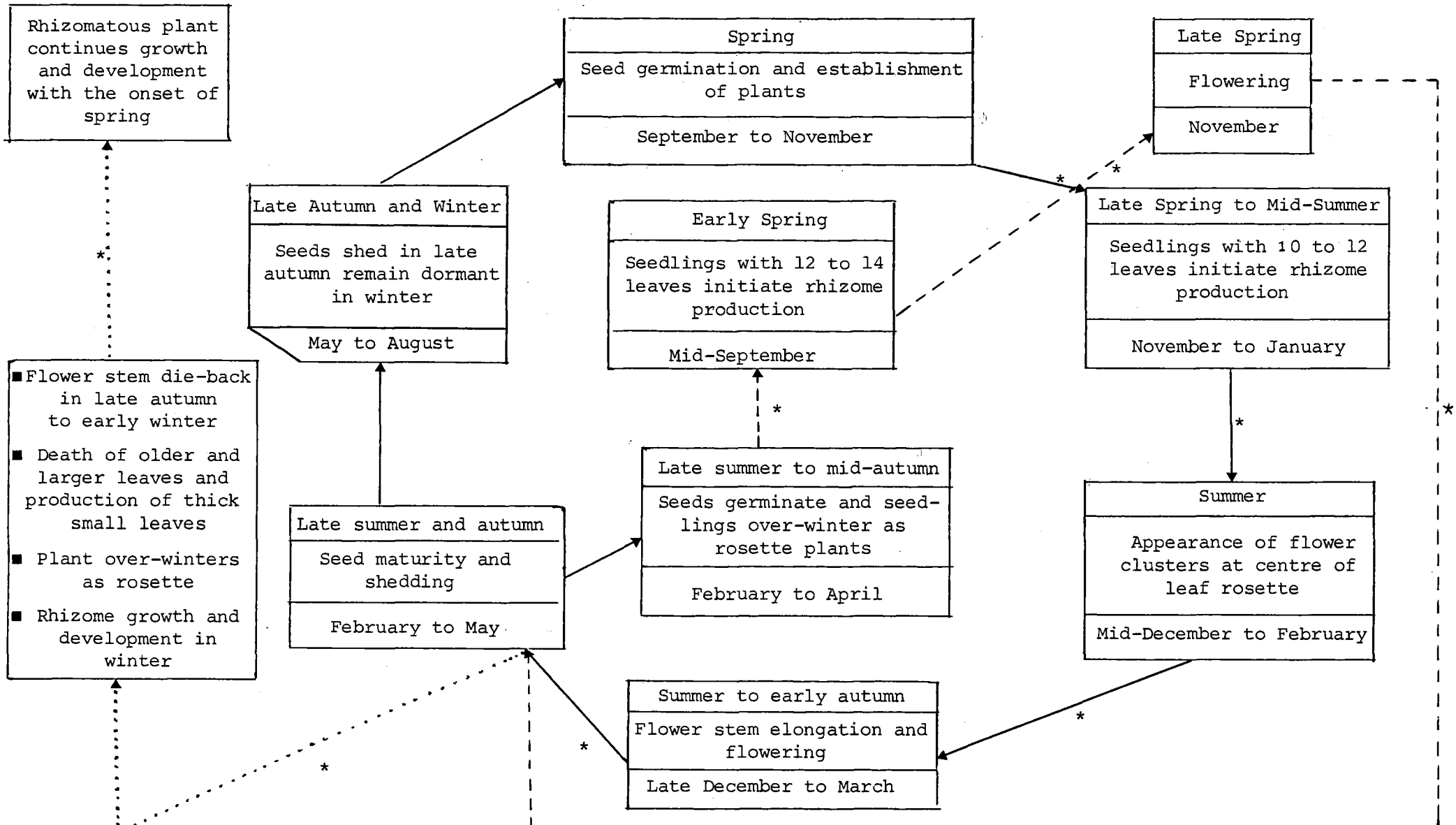
#Seed dried to constant weight at 30C.

APPENDIX 15

Life history of spring (——▶) and autumn (- - - -▶) germinating seedling yarrow.

* Vegetative/rhizome-growth and development.

·····▶ Growth and development of the parent plant after seed maturity.


Rhizomatous plant continues growth and development with the onset of spring
Spring
Seed germination and establishment of plants
September to November
Late Spring
Flowering
November
Late Autumn and Winter
Seeds shed in late autumn remain dormant in winter
May to August
Early Spring
Seedlings with 12 to 14 leaves initiate rhizome production
Mid-September
Late Spring to Mid-Summer
Seedlings with 10 to 12 leaves initiate rhizome production
November to January
Flower stem die-back in late autumn to early winter
Death of older and larger leaves and production of thick small leaves
Plant over-winters as rosette
Rhizome growth and development in winter
Late summer and autumn
Seed maturity and shedding
February to May
Late summer to mid-autumn
Seeds germinate and seed-lings over-winter as rosette plants
February to April
Summer
Appearance of flower clusters at centre of leaf rosette
Mid-December to February
Summer to early autumn
Flower stem elongation and flowering
Late December to March

Appendix 16: The procedure of chemical analysis of the yarrow, barley and pea plant material to determine N, P and K levels (Chapter 5).

Reagents and Standards

1. 0.1 N sodium hydroxide solution (for autoanalyser dilution and neutralization).

2. Vanadomolybdate KMV solution (for P determination):

   (i) 12 g ammonium molybdate was dissolved in 140 ml distilled water by warming to 50°C and the solution was allowed to cool to room temperature.

   (ii) 88 ml of concentrated nitric acid was added to 250 ml distilled water.

   (iii) The cooled solution of ammonium molybdate (i) was added to the nitric acid solution (ii) and mixed well.

   (iv) 2.5 g of ammonium metavanadate was dissolved in 100 ml of 0.2 N sodium hydroxide.

   (v) 24 ml of the ammonium metavanadate solution (iv) was added to the ammonium molybdate/nitric acid solution (iii) and mixed well.

3. 2.8 N sodium hydroxide solution (for P determination).

4. Catalyst (for Kjeldahl digestion).

   1 g elemental selenium (LR) was thoroughly mixed with 100 g anhydrous sodium sulphate (AR).

5. Concentrated sulphuric acid (AR) (for Kjeldahl digestion).

6. Standards.

   (i) Stock matrix solution:

   20 ml concentrated and 15.5 g of anhydrous sodium sulphate mixed in a 100 ml volumetric flask and the solution was made up to the 100 ml mark. No elemental selenium was added.

(ii) Stock composite solution:

471.65, 43.9 and 170.25 mg of ammonium sulphate, potassium dihydroxen phosphate, and potassium chloride, respectively, were dissolved in 100 ml distilled water. This solution had 100, 10, and 100 mg N, P and K,respectively.

(iii) Working series solutions (working standards):

(a) 0, 2, 4, 6, and 8 ml of the stock composite was pipetted severally, into separate 100 ml volumetric flasks.

(b) 10 ml of stock matrix solution was added into each volumetric flask and made up to the 100 ml mark.

Procedure

(i) Sample preparation:

(a) The shoot material of each plant species, from each treatment, was ground separately into a fine powder using a 'cyclone' electric grinder.

(b) The ground plant material was oven dried to a constant weight at $80^{o}C$.

(ii) Kjeldahl digestion:

(a) 0.1 g of ground and oven dried plant material from each treatment was weighed and transferred into separate 100 ml 'Tecator' digestion tubes.

(b) Approximately 1.5 g of the catalyst (4) and 3 ml concentrated sulphuric acid (6) were added into each of the above digestion tubes.

(c) These digestion tubes were then heated for 1.5 h at $420^{o}C$, until the charring disappeared, and for a further 1.5 h at $240^{o}C$ and then allowed to cool to room temperature before making up to a 100 ml mark with distilled water.

(iii) Analysis:

(a) Nitrogen (N)

Aliquots from each digest solution (sample standard) were run through an autoanalyser to determine N. Before and after each run of a sample standard, the series of working standards were run as checks.

(b) Phosphorus (P)

(i) To 20 ml of each sample standard and working standard, 5 ml of 2.8 N sodium hydroxided (3) was added and mixed well. Then, 5 ml of KMV reagent (1) was added into each standard and mixed well. These solutions were allowed to stand for 15 minutes.

(ii) Light absorbance at 420 nm was measured in each of the above solutions, using a Shimadzu uv 110 spectrophotometer.

(c) Potassium (K)

(i) To 5 ml of each sample standard and working standard, 15 ml of distilled water was added.

(ii) Atomic absorption or emission at 766.7 nm was measured in each of the above solutions using an air-acetylene flame.

Calculation of total N-P-K in plant material

The amounts of N, P, and K present in the total plant material of each species, in each treatment, was calculated by substituting their appropriate values in the following generalized formula:

$$\frac{n}{0.1} \times y$$

where n = mg of N, P or K present in 0.1 g of the plant material,

y = total dry weight of plant material.

Appendix 17: The per plant yields* of dry weight, nitrogen, phosphorus, and potassium of yarrow and crop# plants grown both in monoculture and in mixtures. (Chapter 5 - Experiments 3 and 4.)

	Mean weight				
	Plant density (number of yarrow plants:number of crop plants				
	4:0	3:1	2:2	1:3	0:4
Dry weight (g)					
Yarrow/barley experiment	0.36	0.20; 2.72	0.11; 2.18	0.08; 1.66	1.41
Yarrow/pea experiment	0.34	0.29; 1.64	0.26; 1.36	0.25; 1.04	0.84
Nitrogen (mg)					
Yarrow/barley experiment	9.18	7.60; 25.70	6.25; 21.30	6.20; 18.47	16.90
Yarrow/pea experiment	9.73	8.57; 83.60	7.95; 65.20	8.20; 49.03	41.80
Phosphorus (mg)					
Yarrow/barley experiment	10.38	9.40; 15.70	8.30; 15.70	8.70; 13.60	13.08
Yarrow/pea experiment	10.20	8.57; 45.40	6.95; 41.35	5.30; 36.03	33.35
Potassium (mg)					
Yarrow/barley experiment	15.33	13.90; 34.60	12.25; 34.55	13.50; 32.10	30.88
Yarrow/pea experiment	15.55	12.63; 54.80	9.95; 46.35	8.70; 39.30	35.10

* Forty-nine days after seedling emergence from the soil.
\# Experiment 3: The crop was barley; Experiment 4: The crop was field peas.

Appendix 18: Partitioned sums of squares of relative yields (obtained by the analysis of variance of the appropriate relative yield data) by the use of orthogonal polynomials#. Significance was tested as 95% probability. (Chapter 5: Experiments 3 and 4.)

Source		d.f.	r_W	r_N	r_P	r_K
(i) Experiment 3						
Yarrow		4	3.940 *	3.670 *	4.144 *	3.619 *
	Linear	1	3.279 *	3.630 *	4.054 *	3.604 *
	Quadratic	1	0.598 *	0.036 *	0.014 *	0.001 *
	Cubic	1	0.057 *	0.003 *	0.068 *	0.009 *
	Quartic	1	0.006 ns	0.001 *	0.008 *	0.005 *
	Error	20	0.083	0.0001	0.00009	0.00002
Barley		4	4.229 *	4.763 *	5.875 *	3.600 *
	Linear	1	3.663 *	3.721 *	3.864 *	3.754 *
	Quadratic	1	0.553 *	1.041 *	2.003 *	1.003 *
	Cubic	1	0.008 ns	0.001 ns	0.005 ns	0.004 ns
	Quartic	1	0.005 ns	0.0001 ns	0.003 ns	0.004 ns
	Error	20	0.108	2.772	1.882	2.763
(ii) Experiment 4						
Yarrow		4	3.895 *	3.792 *	3.649 *	3.762 *
	Linear	1	3.680 *	3.769 *	3.577 *	3.730 *
	Quadratic	1	0.214 *	0.020 *	0.054 *	0.030 *
	Cubic	1	0.001 ns	0.002 *	0.013 *	0.001 ns
	Quartic	1	0.001 ns	0.001 *	0.005 *	0.001 ns
	Error	20	0.045	0.003	0.003	0.007
Peas		4	3.729 *	3.900 *	3.636 *	3.522 *
	Linear	1	3.375 *	3.437 *	3.441 *	3.242 *
	Quadratic	1	0.306 *	0.433 *	0.147 *	0.207 *
	Cubic	1	0.038 *	0.027 *	0.037 *	0.065 *
	Quartic	1	0.010 ns	0.003 *	0.011 *	0.009 *
	Error	20	0.046	0.007	0.009	0.008

Method of partitioning of sums of squares is detailed in Steel and Torrie (1960).

Appendix 19: Partitioned sums of squares of relative yield totals (obtained by the analysis of variance of the appropriate RYT data) by the use of orthogonal polynomials#. Significance was tested at 95% probability. (Chapter 5: Experiments 3 and 4[√].)

Source	d.f.	RYT_W	RYT_N	RYT_P	RYT_K
(i) Yarrow/barley experiment					
RYT	4	0.0746 *	0.00037 ns	0.001753 ns	0.000067 ns
Linear	1	0.0697 *	0.00026 *	0.001643 *	0.000058 *
Quadratic	1	0.0048 *	0.00008 ns	0.000090 ns	0.000007 ns
Cubic	1	0.0001 ns	0.00002 ns	0.000015 ns	0.000002 ns
Quartic		0.00003 ns	0.000005 ns	0.000005 ns	0.000000 ns
Error	20	0.0032	0.00076	0.00724	0.000253
(ii) Yarrow/pea experiment					
RYT	4	0.1796534 *	0.2033867 *	0.0028827 ns	0.0027467 ns
Linear	1	0.0016017 *	0.0022817 *	0.0026923 *	0.0025732 *
Quadratic	1	0.1710012 *	0.1914298 *	0.0001702 ns	0.0001627 ns
Cubic	1	0.0064067 *	0.0091266 *	0.0000151 ns	0.0000106 ns
Quartic	1	0.0006438 *	0.0005486 *	0.0000051 ns	0.0000002 ns
Error	20	0.0040667	0.0026533	0.0063257	0.0154743 ns

Method of partitioning of sums of squares is detailed in Steel and Torrie (1960).

√ Experiment 3: (i); Experiment 4: (ii).

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REFERENCES

ABRAHAMSON, W.G. 1979. Patterns of resource allocation in wild flower populations of fields and woods. *American Journal of Botany 66:* 71-79.

ACOCK, B.; THORNLEY, J.H.M.; WILSON, J.W. 1970. Spatial variation of light in the canopy. p. 91-101. In: Setlik, I. (ed.). *Prediction and measurement of photosynthetic productivity.* Proceedings of the IBP/PP Technical meeting, 1969, Wageningen, Pudoc.

AMEN, R.D. 1966. The extent and role of seed dormancy in alpine plants. *Quarterly Review of Biology 41:* 271-281.

AMEN, R.D. 1968. A model of seed dormancy. *Botanical Review 34:* 1-31.

ANDERSON, J.D. 1973. Metabolic changes associated with senescence. *Seed Science and Technology 1:* 401-416.

ANDREWS, R.E.; NEWMAN, E.I. 1970. Root density and competition for nutrients. *Oecol. Plant. Gauthier-Villars 5:* 319-334.

ASPINALL, D. 1960. An analysis of competition between barley and white persicaria. II. Factors determining the course of competition. *Annals of Applied Biology 48:* 637-654.

ASPINALL, D.; MILTHORPE, F.L. 1959. An analysis of competition between barley and white persicaria. I. The effects on growth. *Annals of Applied Biology 47:* 156-172.

BALLARD, L.A.T. 1973. Physical barriers to germination. *Seed Science and Technology 1:* 285-303.

BARLEY, K.P. 1970. The configuration of the root system in relation to nutrient uptake. *Advances in Agronomy 22:* 159-201.

BARRETT, D.W.; CAMPBELL, N.A. 1974. An evaluation of the effects of competition between wheat and Wimmera ryegrass (*Lolium rigidum*) during early stages of growth. *Australian Journal of Experimental Agriculture and Animal Husbandry 13:* 581-586.

BENEDICT, H.M. 1941. Growth of some range grasses in reduced light. *Botanical Gazette 102:* 582-589.

BIBBEY, R.O. 1948. Physiological studies of weed seed germination. *Plant Physiology 23:* 467-484.

BLACK, C.C.; CHEN, T.M.; BROWN, R.H. 1969. Biochemical basis for plant competition. *Weed Science 17:* 338-344.

BLACK, J.N. 1957. The influence of varying light intensities on the growth of herbage plants. *Herbage Abstracts 27:* 89-98.

BLACK, J.N. 1958. Competition between plants of different initial seed size in swards of Subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light micro-climate. *Australian Journal of Agricultural Research 9:* 299-318.

BLACK, J.N. 1960. The significance of petiole length, leaf area, and light interception in competition between strains of Subterranean clover (*Trifolium subterraneum* L.) grown in swards. *Australian Journal of Agricultural Research 11:* 277-291.

BLACK, M. 1959. Dormancy studies of seeds of *Avena fatua*. I. The possible role of germination inhibitors. *Canadian Journal of Botany 37:* 393-402.

BLACKMAN, G.E.; TEMPLEMAN, W.G. 1938. The nature of competition between cereal crops and annual weeds. *Journal of Agricultural Science 28:* 247-271.

BLACKMAN, V.H. 1919. The compound interest law and plant growth. *Annals of Botany 33:* 353-360.

BLACKMAN, G.E.; BLACK, J.N. 1959. Physiological and ecological studies in the analysis of plant environment. XI. A further assessment of the influence of shading on the growth of different species in the vegetative phase. *Annals of Botany 23:* 51-63.

BLACKMAN, G.E.; WILSON, G.L. 1951a. Physiological and ecological studies in the analysis of plant environment. VI. The constancy for different species of a logarithmic relationship between net assimilation rate and light intensity and its ecological significance. *Annals of Botany XV:* 63-94.

BLACKMAN, G.E.; WILSON, G.L. 1951b. Physiological and ecological studies in the analysis of plant environment. VII. An analysis of the differential effects of light intensity on the net assimilation rate, leaf area ratio, and relative growth rate of different species. *Annals of Botany XV:* 373-408.

BLASER, R.E.; BRADY, N.C. 1950. Nutrient competition in plant associations. *Agronomy Journal 42:* 128-135.

BLASER, R.E.; TAYLOR, T.; GRIFFITH, W.; SKRDLA, W.H. 1956. Seedling competition in establishing forage plants. *Agronomy Journal 48:* 1-6.

BOSTOCK, S.J. 1978. Seed germination strategies of five perennial weeds. *Oecologia 36:* 113-126.

BOSTOCK, S.J.; BENTON, R.A. 1979. The reproductive strategies of five perennial compositae. *Journal of Ecology 67:* 91-107.

BOURDOT, G.W. 1980. *A study of growth and development of yarrow (Achillea millefolium L.).* Thesis, Ph.D., Lincoln College, University of Canterbury, New Zealand. 293 p.

BOURDOT, G.W. 1982. Yarrow: rhizome control by cultivation. *Proceedings of the 35th New Zealand Weed and Pest Control Conference:* 70-74.

BOURDOT, G.W.; BUTLER, J.H.B. 1981. A relationship between seed yield of white clover and density of yarrow. *Proceedings of the 34th New Zealand Weed and Pest Control Conference:* 37-38.

BOURDOT, G.W.; FIELD, R.J.; WHITE, J.G.H. 1982. Yarrow: numbers of buds in the soil and their activity on rhizome fragments of varying length. *New Zealand Journal of Experimental Agriculture 10:* 63-67.

BOURDOT, G.W.; WHITE, J.G.H.; FIELD, R.J. 1979. Seasonality of growth and development in yarrow. *Proceedings of the 32nd New Zealand Weed and Pest Control Conference:* 49-54.

BOWEN, J.E. 1973. Kinetics of zinc absorption by excised roots of two sugar cane clones. *Plant Soil 39:* 125-129.

BRAY, R.H. 1954. A nutrient mobility concept of soil-plant relationships. *Soil Science 78:* 9-22.

BRIGGS, G.E.; KIDD, F.; WEST, C. 1920. A quantitative analysis of plant growth. Parts I and II. *Annals of Applied Biology 7:* 103-123 and 202-223.

BROUGHAM, R.W. 1958. Interception of light by the foliage of pure and mixed stands of pasture plants. *Australian Journal of Agricultural Research 9:* 39-52.

BURTON, G.W.; JACKSON, J.E.; KNOX, F.E. 1959. The influence of light reduction upon the production, persistence, and chemical composition of coastal bermudagrass, *Cynodon dactylon*. *Agronomy Journal 51:* 537-542.

BUTLER, W.L.; NORRIS, K.H.; SIEGELMAN, H.W.; HENDRICKS, S.B. 1959. Detection, assay and preliminary purification of the pigment controlling photoresponsive development of plants. *Proceedings of the National Academy of Sciences, Washington 45:* 1703-1708.

CAPLENOR, D. 1964. Growth and survival of bitterweed, *Helenium amarum,* in relation to nutrition and competitors. *Ecology 45:* 873-876.

CAUSTON, D.R.; VENUS, J.C. 1981. *The Biometry of Plant Growth.* Edward Arnold: London, 307 p.

CHAMBLEE, D.S. 1958. Some above- and below-ground relationships of an alfalfa-orchard grass mixture. *Agronomy Journal 50:* 434-437.

CHANCELLOR, R.J. 1968. The value of biological studies in weed control. *Proceedings of the 9th British Weed Control Conference:* 1129-1135.

CHANCELLOR, R.J. 1970. Biological background to the control of three perennial broad-leaved weeds. *Proceedings of the 10th British Weed Control Conference:* 1114,1120

CHANDLER, R.F.; HOOPER, S.N.; HARVEY, M.J. 1982. Ethnobotany and phytochemistry of yarrow, *Achillea millefolium,* compositae. *Economic Botany 36:* 203-223.

CLAPHAM, A.R.; TUTIN, T.G.; WARBURG, E.F. 1962. *Flora of the British Isles.* 2nd ed. Cambridge University Press, 1269 p.

CLAUSEN, J.; KECK, D.D.; HIESEY, W.M. 1958. Experimental studies on the nature of species. III. Environmental responses of climatic races of Achillea. *Carnegie Institute of Washington publication 581.* Baltimore: The Lord Baltimore Press. 129 p.

CLEMENTS, F.E.; WEAVER, J.E.; HANSON, H.C. 1929. Competition in cultivated crops. *Carnegie Institute of Washington publication 398:* 202-233.

COCKAYNE, L. 1920. An economic investigation of the montane tussock-grassland of New Zealand. VIII. An experiment in Central Otago concerning the relative palatability for sheep of various pasture plants. *New Zealand Journal of Agriculture 21:* 176-188.

COHEN, D. 1970. The expected efficiency of water utilisation in plants under different competition and selection regimes. *Israel Journal of Botany 19:* 50-54.

COME, D.; TISSAOUI, T. 1973. Interrelated effects of imbibition, temperature, and oxygen on seed germination. P. 157-168. In: Heydecker, W. (ed.). Seed Ecology. *Proceedings of the Nineteenth Easter School of Agricultural Science,* University of Nottingham, 1972. London: Butterworths.

COOMBE, D.E. 1965. The seasonal light climate and plant growth in a Cambridgeshire Wood, p. 148-166. In: Bainbridge, R.; Evan, G.C.; Rackham, O. *Light as an ecological factor,* Oxford: Blackwell Scientific Publications.

CUSSANS, G.W. 1970. Biological background to the control of rhizomatous grasses. *Proceedings of the 10th British Weed Control Conference:* 1101-1107.

DAWSON, J.H.; BRUNS, V.F. 1975. Longevity of barnyardgrass, green foxtail, and yellow foxtail seeds in soil. *Weed Science 23:* 437-440.

DONALD, C.M. 1951. Competition among pasture plants. I. Intraspecific competition among annual pasture plants. *Australian Journal of Agricultural Research 2:* 355-376.

DONALD, C.M. 1958. The interaction of competition for light and for nutrients. *Australian Journal of Agricultural Research 9:* 421-435.

DONALD, C.M. 1963. Competition among crop and pasture plants. *Advances in Agronomy 15:* 1-118.

DORPH-PETERSON, K. 1925. Examinations of the occurrence and vitality of various weed seed species under different conditions made at the Danish State Seed Testing Station during the years 1896 to 1923. *Report 4th International Seed Testing Congress:* 124-138.

DREW, M.C.; NYE, P.H. 1969. The supply of nutrient ions by diffusion to plant roots in soil. II. The effect of root hairs on the uptake of potassium by roots of rye grass. *Plant Soil 31:* 407-424.

EAGLES, C.F. 1972. Competition for light and nutrients between natural populations of *Dactylis glomerata. Journal of Applied Ecology 9:* 141-152.

ESAHI, Y.; LEOPOLD, A.C. 1968. Physical forces in dormancy and germination of Xanthium seeds. *Plant Physiology 43:* 871-876.

EVANS, L.T. 1969. *The induction of flowering: Some case histories.* MacMillan, 488 p.

EUSSEN, J.H.H. 1978. *The effects of light intensity on some growth characteristics of alangalang (Imperata cylindrica (L.)* Beauv.). BIOTROP, Bogor, Indonesia.

EVANS, G. 1960. Seed multiplications. The influence of water table, soil depth, and soil type on the survival of certain crop and weed seeds. In: *Report of the Welsh Plant Breeding Station for 1959.* Aberystwyth, University College of Wales. 60 p.

EVANS, G.C.; HUGHES, A.P. 1961. Plant growth and the aerial environment. I. Effect of artificial shading on *Impatiens parviflora. The New Phytologist 60:* 150-180.

EVANS, P.S. 1978. Plant root distribution and water use patterns of some pasture and crop species. *New Zealand Journal of Agricultural Research 21:* 261-265.

EVENARI, M. 1949. Germination inhibitors. *Botanical Review 15:* 153-194.

EVENARI, M. 1965. Light and seed dormancy. *Encyclopaedia of Plant Physiology 15:* 804-847.

FENNER, M. 1978. Susceptibility to shade in seedlings of colonizing and closed turf species. *The New Photologist 81:* 739-744.

FIELD. R.J. 1982. (Personal communication.)

FISHER, N.M. 1979. Studies in mixed crpping. III. Further results with maize-bean mixtures. *Experimental Agriculture 15:* 49-58.

FRANKLAND, B. 1976. Phytochrome control of seed germination in relation to the light environment. p. 477-492. In: Smith, H. (ed.). *Light and Plant Development.* London: Butterworths. 516 p.

FRANKLAND, B.; WAREING, P.F. 1966. Hormonal regulation of seed development in Hazel (*Corylus avellana* L.) and Beech (*Fabus sylvatica* L.). *Journal of Experimental Botany 17:* 596-611.

FRIEDMAN, J. 1971. The effect of competition by adult *Zygophyllum clumosum* Boiss. on seedlings of *Artemesia herba-alba* Asso. in the Neger desert of Israel. *Journal of Ecology 59:* 775-782.

GRAY, A. 1950. *Handbook of flowering plants and ferns of the central and north-eastern United States and adjacent Canada.* 8th ed. New York: D. Van Nostrand Company.

GRAY, B.; DRAKE, M.; COLBY, W.G. 1953. Potassium competition in grass-legume associations as a function of root cation exchange capacity. *Proceedings of the Soil Science Society of America 17:* 235-239.

GREGORY, F.G. 1917. Physiological conditions in cucumber houses. *Experimental and Research Station 3rd Annual Report:* 19-28. Cheshunt: England.

GRIME, J.P. 1965. Shade tolerance in flowering plants. *Nature,* London. *208:* 161-163.

GRIME, J.P.; JEFFREY, D.W. 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology 53:* 621-642.

GRONER, M.G. 1974. Intraspecific allelopathy in *Kalanchoe daigremontiana*. *Botanical Gazette 135:* 73-79.

GUTTERMAN, Y. 1973. Differences in the progeny due to daylength and hormone treatment of the mother plant. p. 59-80. In: Heydecker, W. (ed.). Seed Ecology. *Proceedings of the Nineteenth Easter School in Agricultural Science,* University of Nottingham, London: Butterworths.

HALL, R.L. 1974a. Analysis of the nature of interference between plants of different species. I. Concept and extension of the De Wit analysis to examine effects. *Australian Journal of Agricultural Research 25:* 739-747.

HALL, R.L. 1974b. Analysis of the nature of interference between plants of different species. II. Nutrient relations in a Nandi *Setaria* and greenleaf *Desmodium* association with particular reference to potassium. *Australian Journal of Agricultural Research 25:* 749-756.

HANF, M. 1974. *Weeds and their Seedlings.* Hadleigh, Ipswich: B.A.S.F., United Kingdom. 348 p.

HARPER, J.L. 1959. The ecological significance of dormancy and its importance in weed control. *Proceedings of the IVth International Congress on Crop Protection 1:* 415-420. Hamburg (1957).

HARPER, J.L. 1961. Approaches to the study of plant competition. p. 1-39. In. Milthorpe, F.L. (ed.). Mechanisms of Biological Competition. *Symposium of the Society of Experimental Biology 15:* Cambridge.

HARPER, J.L. 1964. The nature and consequence of interference amongst plants. In: Genetics Today. *Proceedings of the 11th International Congress of Genetics 2:* 465-482.

HARPER, J.L. 1977. *Population Biology of Plants.* Academic Press, 892 p.

HARPER, J.L.; CLATWORTHY, J.N. 1963. The comparative biology of closely-related species. VI. Analysis of the growth of *Trifolium repens* and *T. fragiferum* in pure and mixed populations. *Journal of Experimental Botany 14:* 172-190.

HARPER, J.L.; GAJIC, D. 1961. Experimental studies of the mortality and plasticity of a weed. *Weed Research 1:* 91-104.

HARPER, J.L.; SAGAR, G.R. 1953. Some aspects of the ecology of buttercups in permanent grassland. *Proceedings of the British Weed Control Conference 1:* 256-265.

HARRIS, G.A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum. Ecology Monograph 37:* 89-111.

HART, P.B.S. 1978. *Some aspects of nitrogen mineralisation in soil under fallow and wheat.* Thesis, M.Agr.Sc., Lincoln College, University of Canterbury, N.Z. 247 p.

HAYNES, R.J. 1980. Competitive aspects of the grass-legume association. *Advances in Agronomy 33:* 227-261.

HEATH, O.V.S.; GREGORY, F.G. 1938. The constancy of mean NAR and its ecological importance. *Annals of Botany 2:* 811-818. (New series.)

HENDRICKS, S.B.; TAYLORSON, R.B. 1972. Promotion of seed germination by nitrates and cyanides. *Nature,* London. *237:* 169-170.

HEYWOOD, V.H.; HUMPHRIES, C.J. 1977. Anthemidea - systematic review. p. 851-898. In: Heywood, V.H.; Harborne, J.B.; Turner, B.L. (eds). *The Biology and Chemistry of the Compositae* Vol. 2. New York. Academic Press.

HILGENDORF, F.W.; CALDER, J.W. 1952. *Weeds of New Zealand and how to eradicate them.* 5th ed. New Zealand: Whitcombe and Tombs. 260 p.

HILL, J. 1973. Methods of analysing competition with special reference to herbage plants. II. Effects of associate plants. *The Journal of Agricultural Science 81:* 91-98. Cambridge.

HILL, J.; SHIMAMOTO, Y. 1973. Methods of analysing competition with special reference to herbage plants. I. Establishment. *The Journal of Agricultural Science 81:* 77-89. Cambridge.

HILL, T.A. 1977. *The Biology of Weeds.* The Institute of Biology's Studies in Biology, No. 79, Edward Arnold: London. 64 p.

HIRANO, S.; KIRA, T. 1965. Influences of autotoxic root exudation on the growth of higher plants grown at different densities (Intraspecific competition among higher plants XII). *Journal of Biology.* Osaka City University 16: 27-44.

HIRANO, S.; MORIOKA, S. 1964. On the inter-relation of the growth retarding activity of the root-excretion among various kinds of fruit trees. *Journal of the Japanese Society of Horticultural Science 33:* 13-22.

HODGSON, G.L.; BLACKMAN, G.E. 1956. An analysis of the influence of plant density on the growth of *Vicia faba.* I. The influence of density on the pattern of development. *Journal of Experimental Botany 7:* 147-165.

HOLLIDAY, R.J. 1960. Plant population and crop yield. *Field Crop Abstracts 13:* 159-167.

HOLM, L.; PANCHO, J.V.; HERBERGER, J.P.; PLUCKNETT, D.L. 1979. *A Geographical Atlas of World Weeds.* Canada: John Wiley. 391 p.

HOVELAND, C.S.; BUCHANAN, G.A.; CROWLEY, R.H.; TEEM, D.H. McGUIRE, J.A. 1978. Response of weed and crop species to shade. In: *Abstracts 1978, Weed Science Society of America, meeting.* Auburn University: Alabama, U.S.A.

HUGHES, A.P. 1959. Effect of the environment of leaf development in *Impatiens parviflora* DC. *Journal of the Linnean Society, Botany 56:* 161-165.

HUGHES, A.P. 1962. Plant growth and the aerial environment. VII. The growth of *Impatiens parviflora* in very low light intensities. *The New Phytologist 64:* 55-64.

HUGHES, A.P. 1965 . Plant growth and the aerial environment. IX. A synopsis of the autecology of *Impatiens parviflora. The New Phytologist 64:* 399-413.

HUGHES, A.P. 1966. The importance of light compared with other factors affecting plant growth. p. 121-146. In: Bainbridge, R.; Evans, G.C.; Rackham, O. (eds). *Light as an ecological factor.* Oxford: Blackwell Scientific Publications.

HUGHES, A.P.; EVANS, G.C. 1962. Plant growth and the aerial environment. II. Effects of light intensity on *Impatiens parviflora*. *The New Phytologist 61:* 154-174.

HUGHES, A.P.; FREEMAN, P.R. 1967. Growth analysis using frequent small harvests. *Journal of Applied Ecology 4:* 553-560.

HUNT, R. 1978. *Plant Growth Analysis.* The Institute of Biology's Studies in Biology, No. 96, Edward Arnold: London. 67 p.

HYDE, E.O.C. 1954. The function of the hilum in some Papilionaceae in relation to the ripening of the seed and the permeability of the testa. *Annals of Botany 18:* 241-256.

IDRIS, H.; MILTHORPE, F.L. 1966. Light and nutrient supplies in the competition between barley and charlock. *Oecol. Plant. 1:* 143-164.

I.S.T.A. 1976. International Rules for Seed Testing. *Seed Science and Technology. Proceedings of the International Seed Testing Association 4:* p. 23.

IVENS, G.W.; MLOWE, F. 1980. A study of competition between seedlings of gorse (*Ulex europaeus* L.) and perennial ryegrass (*Lolium perenne* L.) by means of a replacement series experiment. *Weed Research 20:* 183-191.

IWAKI, H. 1959. Ecological studies on interspecific competition in a plant community. I. An analysis of growth of competing plants in mixed stands of buckwheat and green gram. *Japanese Journal of Botany 17:* 120-138.

JACKMAN, R.H.; MOUAT, M.C.H. 1972a. Competition between grass and clover for phosphate. I. Effect of browntop (*Agrostis tenuis* Sibth.) on white clover (*Trifolium repens* L.) growth and nitrogen fixation. *New Zealand Journal of Agricultural Research 15:* 653-666.

JACKMAN, R.H.; MOUAT, M.C.H. 1972b. Competition between grass and clover for phosphate. II. Effect of root activity, efficiency of response to phosphate, and soil moisture. *New Zealand Journal of Agricultural Research 15:* 667-675.

JUSTICE, O.L. 1973. Introductory remarks. *Seed Science and Technology 1:* 399-400.

KEELEY, P.E.; THULLEN, R.J. 1978. Light requirements of yellow nutsedge (*Cyperus esculentus*) and light interception by crops. *Weed Science 21:* 10-16.

KHAN, A.A. 1977. Seed dormancy: changing concepts and theories. p. 29-50. In: Khan, A.A. (ed.). *The physiology and biochemistry of seed dormancy and germination.* Amsterdam:North Holland Publishing Company, 447 p.

KIMBER, R.W.L. 1973. Phytotoxicity from plant residues. III. The relative effect of toxins and nitrogen immobilization on the germination and growth of wheat. *Plant Soil 38:* 543-555.

KING, J. 1971. Competition between established and newly-sown grass species. *Journal of the British Grassland Society 26:* 221-229.

KIVILAAN, A.; BANDURSKI, R.S. 1973. The ninety year period for Dr Beal's seed viability experiment. *American Journal of Botany 60:* 140-145.

KNAKE, E.L. 1972. Effect of shade on giant foxtail. *Weed Science 30:* 588-592.

KNUTH, P. 1908. *Achillea millefolium* L. p. 611-616. In: Knuth, P. *Handbook of Flower Pollination.* Oxford: Clarendon Press.

KOLLER, D. 1962. Preconditioning of germination in lettuce at time of fruit ripening. *American Journal of Botany 49:* 841-844.

KOOSTRA, P. 1973. Changes in seed ultrastructure during senescence. *Seed Science and Technology 1:* 417-425.

KORSMO, E. 1954. *Achillea millefolium* L. p. 327-330. In: Korsmo, E. *Anatomy of Weeds.* Norway: Kirstes Boktrykkeri.

KVET, J.; ONDOK, J.P.; NECAS, J.; JARVIS, P.G. 1971. Methods of growth analysis. p. 343-391. In: Sestak, Z.; Catsky, J.; Jarvis, P.G. (eds). *Plant photosynthetic production: Manual of Methods.* Junk, W., The Hague.

LACROIX, L.J.; JASWAL, A.S. 1973. Lipid and sugar metabolism during after-ripening of sour cherry embryos. *Canadian Journal of Botany 51:* 1267-1270.

LAMBERT, D.A. 1967. Competition between plants of cocksfoot (*Dactylis glomerata*) grown for seed. *Journal of the British Grassland Society 23:* 274-279.

LANG, A.L.; PENDLETON, J.W.; DUNGAN, G.H. 1956. The influence of population and nitrogen level on yield and protein contents of nine corn hybrids. *Agronomy Journal 48:* 284-289.

LANGER, R.H.M. 1973. Growth of grasses and clovers, p. 42-63. In: R.H.M. Langer (ed.). *Pastures and Pasture Plants.* Wellington: A.H. and A.W. Reed.

LASKEY, B.C.; WAKEFIELD, R.C. 1978. Competitive effects of several grass species and weeds on the establishment of birdsfoot trefoil. *Agronomy Journal 70:* 146-148.

LEVY, E.B. 1931. Weeds in lawns and greens. Competition effects and control by treatment with chemical sprays. *New Zealand Journal of Agriculture 42:* 406.

LEWAK, S.; RUDNICKI, R.M. 1977. After-ripening in cold requiring seeds. p. 193-217. In: Khan, A.A. (ed.). *The physiology and biochemistry of seed dormancy and germination.* Amsterdam: North Holland Publishing Company. 447 p.

LEWIS, J. 1961. The influence of water level, soil depth, and soil type on the survival of crop and weed seeds. *Proceedings of the International Seed Testing Association 26:* 65-68.

LEWIS, J. 1973. Longevity of crop and weed seeds. Survival after 20 years in soil. *Weed Research 13:* 179-191.

LITAV, M.; ISTI, D. 1974. Root competition between two strains of *Spinacia oleracea*. I. Pattern and Processes. *Journal of Applied Ecology 11:* 1007-1016.

LITAV, M.; SELIGMAN, N. 1969. Competition between *Oryzopsis holciformis* (M.B.) Hack. and annual plants. I. Performance of *Oryzopsis* as affected by presence of annuals, nutrient supply, and differential sowing times. *Israel Journal of Botany 18:* 149-169.

LITAV, M.; WOLOVITCH, S. 1971. Partial separation of roots as a means of reducing the effect of competition between two grass species. *Annals of Botany 35:* 1163-1178.

LOACH, K. 1967. Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. *The New Phytologist 66:* 607-621.

MANN, H.H.; BARNES, T.W. 1947. Competition between barley and certain weeds under controlled conditions. II. Competition with *Holcus mollis*. *Annals of Applied Biology 34:* 252-264.

MARTIN, M.P.L.D. 1982. (Personal communication.)

MARTIN, M.P.L.D.; SNAYDON, R.W. 1982. Root and shoot interactions between barley and field beans when intercropped. *Journal of Applied Ecology 19:* (in press).

MATTHEWS, L.J. 1975. *Weed control by chemical methods.* 2nd ed. Wellington: Government Printer, 710 p.

MATTHEWS, L.J. 1976. The Journal Guide to Weed Control. I. Pasture weeds. *New Zealand Journal of Agriculture 133:* 38-47.

MAYER, A.M.; POLJAKOFF-MAYBER, A. 1975. *The germination of seeds.* Oxford: Pergamon Press, 192 p.

McCOWN, R.L.; WILLIAMS, W.A. 1968. Competition for nutrients and light between the annual grassland species *Bromus mollis* and *Erodium botrys*. *Ecology 49:* 981-990.

McGILCHRIST, C.A. 1965. Analysis of competition experiments. *Biometrics 21:* 975-985.

McGILCHRIST, C.A.; TRENBATH, B.R. 1971. A revised analysis of competition experiments. *Biometrics 27:* 659-671.

McPHERSON, J.K.; MULLER, C.H. 1969. Allelopathic effects of *Adenostoma faciculatum,* "Chamise", in the California chaparral. *Ecological Monograph 39:* 177-198.

McWHORTER, C.G.; JORDAN, T.N. 1976. The effect of light and temperature on the growth and development of johnsongrass. *Weed Science 24:* 88-91.

MILTHORPE, F.L. 1961. The nature and analysis of competition between plants of different species. p. 330-355. In: Mechanisms in biological competition. *Symposia of the Society of Experimental Biology* No. XV. Cambridge : University Press.

MITCHELL, K.J. 1954. Influence of light and temperature on the growth of ryegrass (*Lolium* spp.). 3. Pattern and rate of tissue formation. In: *Physiology, Plant 6:* 21-46.

MONTEITH, J.L.; SZEICZ, G. 1960. The carbon-dioxide flux over a field of sugar beet. *Quarterly Journal of the Royal Meteorological Society 86:* 205-214.

OSIRU, D.S.O.; WILLEY, R.W. 1972. Studies on mixtures of dwarf sorghum and beans (*Phaseolus vulgaris*) with particular reference to plant population. *Journal of Agricultural Science, Cambridge 79:* 531-540.

OSIRU, D.S.O.; WILLEY, R.W. 1976. Studies on mixtures of maize and beans with particular emphasis on the time of planting beans. *Symposium on Intercropping in Semi-Arid Areas,* Morogoro, Tanzania.

OVERLAND, L. 1966. The role of allelopathic substances in the "smother crop" barley. *American Journal of Botany 53:* 423-432.

MORAL, R. DEL; MULLER, C.H. 1969. Fog drip: a mechanism of toxin transport from *Eucalyptus globulus*. *Bulletin of the Torrey Botanical Club 98:* 467-475.

MOUAT, M.C.H.; WALKER, T.W. 1959. Competition for nutrients between grasses and white clover. I. Effect of grass species and nitrogen supply. *Plant and Soil 11:* 30-40.

NICHOLLS, A.J.; CALDER, D.M. 1973. Comments on the use of regression analysis for the study of plant growth. *The New Phytologist 72:* 571-581.

NIETO, J.H.; STANIFORTH, D.W. 1961. Corn-foxtail competition under various production conditions. *Agronomy Journal 53:* 1-5.

NIKOLAEVA, M.G. 1977. Factors controlling the seed dormancy pattern p. 51-74. In: Khan, A.A. (ed.). *The physiology and biochemistry of seed dormancy and germination*. Amsterdam: North Holland Publishing Company, 447 p.

NOGUCHI, K.; NAKAYAMA, K. 1978a. Studies on competition between upland crops and weeds. 3. Effect of shade on growth of weeds. *Japanese Journal of Crop Science 48:* 56-62.

NOGUCHI, K.; NAKAYAMA, K. 1978b. Studies on competition between upland crops and weeds. 4. Changes of light environment in crop canopies and hypothesis about the period for weed-free maintenance. *Japanese Journal of Crop Science 48:* 381-387.

NORMAN, J.M.; MILLER, E.E.; TANNER, C.B. 1971. Light intensity and sunfleck-size distribution in plant canopies. *Agronomy Journal 63:* 743-748.

OLSEN, S.R.; KEMPLER, W.D. 1968. Movement of nutrients to plant roots. *Advances in Agronomy 20:* 91-151.

PACKHAM, J.R.; WILLIS, A.J. 1977. The effects of shading on *Oxalis acetosella*. *Journal of Ecology 65:* 619-642.

PANDEY, B.N.; SINHA, R.P. 1977. Light as a factor in the growth and morphogenesis. I. Effect of artificial shading on *Crotalaria juncea* L. and *C. sericea* Retz. *The New Phytologist 79:* 431-439.

PANETTA, F.D. 1977. The effect of shade upon seedling growth in groundsel bush (*Baccharis halmifolia* L.). *Australian Journal of Agricultural Research 28:* 681-690.

PATTERSON, D.T. 1980. Shading effects on growth and partitioning of plant biomass in Cogongrass (*Imperata cylindrica*) from shaded and exposed habitats. *Weed Science 28:* 735-740.

PATTERSON, D.T. 1982. Shading responses of purple and yellow nutsedges (*Cyperus rotundus* and *C. esculentus*). *Weed Science 30:* 25-30.

PENDLETON, J.W.; SEIF, R.D. 1962. Role of height in corn competition. *Crop Science 2:* 154-156.

POLLOCK, B.M.; OLNEY, H.O. 1959. Studies of the rest period. I. Growth, translocation and respiratory changes in the embryonic organs of the after-ripening cherry seed. *Plant Physiology 34:* 131-142.

POPAY, A.I.; ROBERTS, E.H. 1970. Ecology of *Capsella bursa-pastoris* (L.) Medik. and *Senecio vulgaris* L. in relation to germination behaviour. *Journal of Ecology 58:* 123-139.

PORTER, N.G.; WAREING, P.F. 1974. The role of oxygen permeabilities of the seed coat in the dormancy of seed of *Xanthium pensylvanicum* Wallr. *Journal of Experimental Botany 25:* 583-594.

PROBST, A.H. 1957. Performance of variety blends in soybeans. *Agronomy Journal 49:* 148-150.

PUTNAM, A.R.; DUKE, W.B. 1974. Biological suppression of weeds: evidence for allelopathy in accessions of cucumber. *Science 185:* 370-371.

RADFORD, P.J. 1967. Growth analysis - Their use and abuse. *Crop Science 7:* 171-175.

RAMPTON, H.H.; CHING, T.M. 1966. Longevity and dormancy in seeds of several cool season grasses and legumes buried in soil. *Agronomy Journal 58:* 220-222.

REMISON, S.U.; SNAYDON, R.W. 1980. A comparison of root competition and shoot competition between *Dactylis glomerata* and *Holcus lanatus*. *Grass and Forage Science 35:* 183-187.

RENNIE, J.C. 1974. Some effects of competition and density of plants on dry weight produced. *Annals of Botany 38:* 1003-1012.

REYNOLDS, D.G. 1961. Yarrow as a weed and seed crop. *New Zealand Journal of Agriculture 102:* 257-258.

ROBERTS, H.A. 1966. The seed population of the soil and its implications for weed control. *Proceedings of the Irish Crop Protection Conference,* 14-22.

SAGAR, G.R. 1968. Factors affecting the outcome of competition between crops and weeds. *Proceedings of the 9th British Weed Control Conference,* 1157-1162.

RHODES, I. 1968. The growth and development of some grass species under competitive stress. 3. The nature of competitive stress and characters associated with competitive ability during seedling growth. *Journal of the British Grassland Society 23:* 330-335.

RHODES, J. 1970a. The production of contrasting genotypes of perennial ryegrass (*Lolium perenne* L.) in monocultures and mixed cultures of varying complexity. *Journal of the British Grassland Society 23:* 156-158.

RHODES, I. 1970b. Competition between herbage grasses. *Herbage Abstracts 40:* 115-121.

RICE, E.L. 1979. Allelopathy - an update. *The Botanical Review 45:* 15-109.

ROBERTS, E.H. 1969. Seed dormancy and oxidation processes. *Symposia of the Society for Experimental Biology 23:* 161-192.

ROBERTS, H.A. 1963. The problem of weed seeds in the soil. *Proceedings of the 2nd Symposium of the British Weed Control Council (1962):* 73-82.

ROBOCKER, W.C. 1977. Germination of seeds of common yarrow (*Achillea millefolium*) and its herbicidal control. *Weed Science 25:* 456-459.

SAEKI, T. 1960. Interrelationships between leaf amount, light distribution and total photosynthesis in a plant community. *Bot. Magazine Tokyo 73:* 55-63.

SAKAI, K.I. 1955. Competition in plants and its relation to selection. *Cold Spring Harbour Symp. Quant. Biol. 20:* 137-157.

SAKAI, K.I. 1961. Competition ability in plants: Its inheritance and some related problems. p. 245-263. Milthrope, F.L. (ed.). *Mechanisms of biological competition.* Symposia of the Society for Experimental Biology 15: Cambridge.

SALISBURY, E.J. 1942. *The reproductive capacity of plants.* London: Bell and Sons.

SANDFAER, J. 1970.. An analysis of the competition between some barley varieties. *Riso Report No. 230.*

SAXBY, S.H. 1944. *Perennial Weeds. New Zealand Journal of Agriculture 68:* 9-12.

SCHAFER, D.E.; CHILCOTE, D.O. 1970. Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. *Crop Science 10:* 342-345.

SCHREIBER, M.M. 1967. A technique for studying weed competition in forage legume establishment. *Weeds 15:* 1-4.

SENDOYA, F.G.; DE DOK, J. 1975. The effect of shade on the growth and development of purple nutsedge (*Cyperus rotandus* L.). From: *Weed Abstracts* (1977) *26:* No. 427.

SHAW, W.C. 1982. Integrated weed management systems technology for pest management. *Weed Science,* supplement to volume 30, 2-12.

SINGH, K.P. 1975. Effect of different light intensities on the growth performance of two ecotypes of *Portulaca oleracea* L. *Tropical Ecology 16:* 163-169.

SINGH, R.N.; MARTENS, D.C.; OBENSHAIN, S.S.; JONES, G.D. 1967. Yield and nutrient uptake by orchard grass as affected by 14 annual applications of N, P and K. *Agronomy Journal 59:* 51-53.

SNAYDON, R.W. 1971. An analysis of the competition between plants of *Trifolium repens* L. populations collected from contrasting soils. *Journal of Applied Ecology 7:* 687-697.

SNAYDON, R.W. 1979. A new technique for studying plant interactions. *Journal of Applied Ecology 16:* 281-286.

STANDARD COMMON NAMES FOR WEEDS IN NEW ZEALAND. 1969. N.Z. Weed and Pest Control Society Publication. New Zealand: Sigma Prints Limited. 141 p.

STEEL, R.G.D.; TORRIE, J.H. 1960. *Principals and Procedures of Statistics.* McGraw-Hill, London. 481 p.

STEINBAUER, G.P.; GRIGSBY, B. 1957. Interaction of temperature, light and moistening agent in the germination of weed seeds. *Weeds 5:* 175-182.

STERN, W.R.; DONALD, C.M. 1962. Light relationships in grass-clover swards. *Australian Journal of Agricultural Research 13:* 599-614.

STOKES, P. 1952. A physiological study of embryo development in *Heracleum sphondylium* L. I. Effect of temperature on embryo development. *Annals of Botany 16:* 572-576.

STOKES, P. 1953. The stimulation of growth by low temperature in *Hercleum sphondylium* L. *Journal of Experimental Botany 4:* 222-234.

STOKES, P. 1965. Temperature and seed dormancy. *Encyclopedia of Plant Physiology 15:* 746-803.

TAYLORSON, R.B. 1970. Changes in dormancy and viability of weed seeds in soils. *Weed Science 18:* 265-269.

TAYLORSON, R.B.; HENDRICKS, S.B. 1977. Dormancy in seeds. p. 331-354. In: *Annual Review of Plant Physiology* 28.

THOMAS, T.H. 1977. Cytokinins, cytokinin-active compounds and seed germination. p. 111-144. In: Khan, A.A. (ed.). *The Physiology and Biochemistry of Seed Dormancy and Germination.* Amsterdam: North-Holland Publishing Company, 447 p.

THOMPSON, K.; GRIME, J.P.; MASON, G. 1977. Seed germination in relation to diurnal fluctuations of temperature. *Nature 267:* 147-149.

THOMPSON, P.A. 1974. Effects of fluctuating temperatures on germination. *Journal of Experimental Botany 25:* 164-175.

THORNTON, N.C. 1935. Factors influencing germination and development of dormancy in cocklebur seeds. *Contr. Boyce Thompson Institute 7:* 477-496.

THURSTON, J.M. 1961. The effect of depth of burying and frequency of cultivation on survival and germination of seeds of wild oats (*Avena fatua* L. and *A. ludoviciana* Dur.). *Weed Research 1:* 19-31.

TOOLE, E.H. 1946. Final results of the Duvel buried seed experiment. *Journal of Agricultural Research 72:* 201-210.

TOOLE, V.K. 1973. Effects of light, temperature, and their interactions on the germination of seeds. *Seed Science and Technology 1:* 339-396.

TOOLE, E.H.; BORTHWICK, H.A.; HENDRICKS, S.B.; TOOLE, V.K. 1953. Physiological studies of the effect of light and temperature on seed germination. *Proceedings of the International Seed Testing Association 18:* 267-276.

TOOLE, E.H.; HENDRICKS, S.B.; BORTHWICK, H.A.; TOOLE, V.K. 1956. Physiology of seed germination. *Annual Review of Plant Physiology 7:* 299-324.

TRENBATH, B.R. 1974. Neighbour effects in the genus *Avena*. II. Comparison of weed species. *Journal of Applied Ecology 11:* 111-125.

TRENBATH, B.R. 1976. Plant interactions in mixed crop communities, p. 129-163. In: *Multiple Cropping*. A.S.A. Special Publication 27 (reprinted 1977). *American Society of Agronomy*.

TROUGHTON, A. 1974. The development of leaf water deficits in plants of *Lolium perenne* in relation to the size of the root and shoot systems. *Plant Soil 40:* 153-160.

TURNER, J.H. 1933. The viability of seeds. *Kew bulletin, Article 34;* 257-269.

VALLIS, J. 1978. Nitrogen relationships in grass/legume mixtures. p. 190-201. In: Wilson, J.R. (ed.). Plant relations in pastures. CSIRO, Melbourne; Australia, 425 p.

VAN DEN BERGH, J.P.; ELBERSE, W.T. 1970. Yields of monocultures and mixtures of two grass species differing in growth habit. *Journal of Applied Ecology 7:* 311-320.

VERGRIS, J.; DRAKE, M.; COLBY, W.G.; BART, J. 1953. Chemical composition of weeds and accompanying crop plants. *Agronomy Journal 45:* 213-218.

VILLIERS, T.A. 1972. Seed dormancy, p. 219-281. In: Koslowski, T.T. (ed.). *Seed Biology*, New York: Academic Press.

VILLIERS, T.A. 1975. *Dormancy and the survival of plants*. The Institute of Biology's Studies in Biology, No. 57. Edward Arnold, London. 67 p.

VILLIERS, T.A.; WAREING, P.F. 1965. The growth-substance content of dormant fruits of *Frazinus excelsior* L. *Journal of Experimental Botany 16:* 533-544.

VINCENT, E.M.; ROBERTS, E.H. 1977. The interaction of light, nitrate, and alternating temperature in promoting the germination of dormant seeds of common weed species. *Seed Science and Technology 5:* 659-670.

VINCENT, E.M.; ROBERTS, E.H. 1979. The influence of chilling, light, and nitrate on germination of dormant seeds of common weed species. *Seed Science and Technology 7:* 3-14.

WALKER, T.W.; ADAMS, A.F.T. 1958. Competition for sulphur in a grass-clover association. *Plant Soil 9:* 353-366.

WAREING, P.F.; FODA, H.A. 1957. Growth inhibitors and dormancy in *Xanthium* seed. *Physiologia Plantarum 10:* 266-280.

WARREN, J.F.; LILL, W.J. 1975. The influence of aerial shields on plant growth environment in competition experiments. *Annals of Botany 39:* 1141-1142.

WARWICK, S.I.; BLACK, L. 1982. The biology of Canadian weeds. 52. *Achillea millefolium* L. S.L. *Canadian Journal of Plant Science 62:* 163-182.

WARWICK, S.I.; BRIGGS, D. 1979. The genecology of lawn weeds. 3. Cultivation experiments with *Achillea millefolium* L., *Bellis perennis* L., *Plantago lanceolata* L., *Plantago major* L. and *Prunella vulgaris* L. collected from lawns and contrasting grassland. habitats. *New Phytologist 83:* 509-536.

WATKINS, D.J. 1940. The growth habits and chemical composition of bromegrass, *Bromus inermis* Leyss., as affected by different environmental conditions. *Journal of the American Society of Agronomy 32:* 527-538.

WATSON, D.J. 1952. The physiological basis of variation in yield. *Advances in Agronomy 4:* 101-144.

WEBB, D.P.; VAN STADEN, J.; WAREING, P.F. 1973. Seed dormancy in *Acer*. Changes in endodgenous cytokinins, gibberellins, and germination inhibitors during the breaking of dormancy in *Acer saccharum* Marsh. *Journal of Experimental Botany 24:* 105-116.

WEBB, L.J.; TRACEY, J.G.; HAYDOCK, K.P. 1967. A factor toxic to seedlings of the same species associated with living roots of the non-gregarious subtropical rain forest tree *Grevillea robusta*. *Journal of Applied Ecology 4:* 13-25.

WEIJER, J. 1952. The colour differences in *Epipactis helleborine* (L). Cr. Wats. and Coult., and the selection of genetical variation by environments. *Genetica 26:* 1-32.

WELBANK, P.J. 1961. A study of the nitrogen and water factors in competition with *Agropyron repens* (L.) Beaux. *Annals of Botany 25:* 116-137.

WELBANK, P.J. 1963. A comparison of competitive effects of some common weed species. *Annals of Applied Biology 51:* 107-125.

WELBANK, P.J. 1964. Competition for N and P in *Agropyron repens*. *Annals of Botany 28:* 1-16.

WHATLEY, J.M.; WHATLEY, F.R. 1980. *Light and Plant Life*. The Institute of Biology's Studies in Biology, No. 124, Edward Arnold, London. 91 p.

WHITEHEAD, F.H.; MYERSCOUGH, P.J. 1962. Growth analysis of plants. The ratio of mean relative growth rate to mean relative rate of leaf area increase. *New Phytologist 61:* 314-321.

WILLEY, R.W.; OSIRU, D.S.O. 1972. Studies on mixture of maize and beans (*Phaseolus vulgaris*) with particular reference to plant population. *Journal of Agricultural Science, Cambridge 28:* 556-580.

WILLIAMS, E.D. 1970. Effects of decreasing the light intensity on the growth of *Agropyron repens* (L). Beauv. in the field. *Weed Research 10:* 360-366.

WILLIAMS, J.T. 1964. A study of the competitive ability of *Chenopodium album* L. I. Interference between kale and *C. album* grown in pure stands and in mixtures. *Weed Research 4:* 283-295.

WILLIAMS, R.F. 1946. The physiology of plant growth with special reference to the concept of net assimilation rate. *Annals of Botany 10:* 41-72 (new series).

WILLIAMS, W.A.; TUCKER, C.L.; GUERRERO, F.P. 1978. Competition between two genotypes of lima beans with morphologically different leaf types. *Crop Science 18:* 62-64.

WIT, C.T. DE. 1960. On competition. *Versl. Landbouwkd. Onderz 66:* 1-82.

WIT, C.T. DE. 1965. Photosynthesis of leaf canopies. *Versl. Landbouwk. Onderz. 663:* 1-57.

✓ WIT, C.T. DE.; TOW, P.G.; ENNIK, G.C. 1966. Competition between legumes and grasses. *Versl. Landbouwk. Onderz. 687:* 3-30.

WIT, C.T. DE; VAN DEN BERGH, J.P. 1965. Competition between herbage plants. *Netherlands Journal of Agricultural Science 13:* 212-221.

WHITTINGTON, W.J. 1973. Genetic regulation of germination, p. 5-31. In: Heydecker, W. (ed.). Seed Ecology. *Proceedings of the Nineteenth Easter School in Agricultural Science*. University of Nottingham. London: Butterworths.