A STUDY OF THE GROWTH AND DEVELOPMENT OF YARROW (*Achillea millefolium* L.)

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Abstract of a thesis submitted for the degree of
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The response of yarrow (*Achillea millefolium* L.) seedlings to reduced light, interference from barley (*Hordeum vulgare*) and some aspects of regeneration from rhizomes were the subject of investigations from 1976 until 1980. Seedlings grown under four intensities of photosynthetically active radiation (100, 46.8, 23.7 and 6.4% of full summer daylight) were harvested on six occasions and the changes with time in the logarithms of leaf area, leaf, stem, root and total dry weights per plant were described by polynomial regression equations. Relative growth rates (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) were derived directly from the growth curves. SLA and LWR increased with increased shading causing LAR to rise, while NAR declined. Response curves of RGR on light intensity, derived from linear regressions of LAR and NAR on the logarithm of relative light intensity predicted maximum RGR to occur at light intensities which decreased with time. This was a consequence of ontogenetic changes in LAR, and changes in NAR apparently related to self shading. Linear regressions of LAR and NAR at a constant total plant dry weight of 1.62 g showed that the increase in LAR almost completely compensated for the reduction in NAR down to approximately 40% full daylight, and maximum RGR was predicted to occur at 59% full daylight. The light compensation point was estimated to be 3.6% full daylight.

Yarrow populations established from 25 and 50 10 cm rhizome fragments m^{-2} were grown alone and with barley at 194 or 359 plants m^{-2}. The barley populations were also grown alone. Growth analysis employing the regression technique, showed the RGR of yarrow was reduced by barley from before jointing (Feekes Scale, Stage 6) as a consequence of reduced NAR. The NAR of yarrow was significantly reduced in the continued presence of barley, which by the time of the final barley harvest resulted in 91 and

and 94% reduction in the accumulated yarrow dry matter at 194 and 359 barley plants m^{-2} respectively. The proportion of total dry matter allocated to seed and rhizome was also reduced by barley but the barley was unaffected by the yarrow. During the autumn and early winter, after removal of the barley, the suppressed yarrow had a higher RGR than the unsuppressed population, owing to higher LAR and NAR. Rhizome growth was vigorous during both autumn and winter in all yarrow populations, but the RGR of rhizome dry matter was higher in the suppressed yarrow during the autumn. This resulted in a progressive reduction in the difference in rhizome dry matter between suppressed and unsuppressed populations.

Several aspects of the development and regenerative potential of rhizomes were investigated. In the first experiment, plants were established from seed and rhizome fragments and harvested on several occasions. Plants from both propagules formed rhizomes on which approximately 97% of axillary buds remained dormant, as long as the plants were undisturbed. Buds on rhizomes attached to the parent plant formed rhizome branches when the apex was damaged, had emerged from the soil, or in situations where internodes were conjested. In the second experiment, rhizome fragments of 4, 8 and 16 cm in length were planted in soil at depths of 0, 2.5, 5.0, 10.0, 20.0 and 30.0 cm. All fragments on the soil surface died without forming shoots owing to desiccation whilst 100% mortality at 20 and 30 cm was probably the result of flooding. Within the 2.5 to 10.0 cm range, an increasing percentage of fragments survived (produced an aerial shoot(s)) as burial depth was reduced and fragment length increased. Within this depth range, the percentage of buds which had become active on undecayed fragments declined with increased length and burial depth. In the third experiment, single-node rhizome pieces were excised from rhizomes retrieved from field populations over a one-year period, and incubated at $25^{o}C$ for 10 days in darkness. More than 90% of buds formed vertical shoots throughout the year, indicating there was no period of innate dormancy in isolated buds. The effect of time of planting on the pattern of early regenerative development was assessed in the fourth experiment, in which 10 cm rhizome fragments were planted at 5 cm depth in soil on two occasions (in November and April). The developmental pattern was the same regardless of month of planting and new

rhizomes were initiated at nodes on the vertical subterranean shoots when 5 to 6 aerial leaves had developed. The planted rhizome fragments declined in dry weight and a minimum weight occurred at about the time when rhizome initiation began.

ERRATA TO A STUDY OF GROWTH AND DEVELOPMENT OF YARROW (*Achillea millefolium* L.)

by

G.W.Bourdot
(1980)

P.8 Dospekhor should be Dospekhov

P.8 Lullukka should be Lallukka

P.9 Cockayne, 1920 a, b are not listed in references. The references are:

COCKAYNE, L. 1920a. 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

COCKAYNE, L. 1920b. An economic investigation of the montane tussock-grassland of New Zealand.IX. Further details regarding the Earnscleugh (Central Otago) palatability experiment. New Zealand Journal of Agriculture 21: 324-334.

P.10 Bruggemann, Bronsch and Drepper (1960) should read Bruggemann, Bronsch, Drepper, Tiews and Gross (1960).

P.277 BRUGGEMAN should read BRUGGEMANN

P.11 (Laszlo, 1954) should read (Laszlo and Henshaw, 1954)

P.16 Hensen (1969) should read Henson (1969)

P.19,22,23 Bostock and Benton (1978) should be Bostock and Benton (1979)

P.21 Dorph-Peterson (1925) should be Dorph-Petersen (1925)

P.280 SALBRIG should read SOLBRIG

P.26 Fuellman and Graber (1938) should read Fuelleman and Graber (1938)

P.27 (Morgon and Klindic, 1973) should read (Morgan and Klindic, 1973)

P.36 Lawerence (1958) should read Lawrence (1958)

P.90,94 (Eagles, 1971a) should read (Eagles,1971)

P.280 EAGLES, C.F. 1971 a. should be EAGLES, C.F.1971

P.90 Warren and Wadsworth (1958) should read Warren Wilson and Wadsworth (1958)

P.276 BICFORD should read BICKFORD

P.168 Hsiao should be Hsia

P.178 (Hakkansson and Wallgren, 1972) should read (Hakansson and Wallgren, 1972)

P.179 (Hakansson, 1972) should read (Hakansson and Wallgren,1972)

P.215 Nigram and McIntyre, 1976) should read Nigram and McIntyre, 1977)

P.230 Yaskonis and Bandzaitene, 1979; should be Yaskonis and Bandzaitene,1970)

P.240 Nicholls and Calder 1972, should be Nicholls and Calder 1973.

P.239 In fifth equation, $e_y f_t^y$

should be $e_y t^y$

In tenth equation, $\frac{1}{RT} \cdot \frac{dRT}{df_t}$ should be

$$\frac{1}{RT} \cdot \frac{dRT}{dt}$$

P.206/208 Values on right hand vertical axis of Figures 5.14 and 5.16 should be 25.0 and 50.0

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PREFACE

The subject of this thesis is the growth and development of yarrow (*Achillea millefolium* L.). The aspects chosen for study were those considered most likely to reveal information that could be employed in developing suitable strategies for controlling the species on arable land. Within the scope of this work are responses to shading and crop competition, the regenerative potential of the rhizomes, and observations on the phenology of the species in Canterbury.

The thesis begins with a broad review of the literature on the species (Chapter 1) followed by a short section describing the structure of the shoot and root systems of the plants used in the investigations (Chapter 2). The following three chapters (Chapters 3, 4 and 5) each have Introduction, Methods, Results and Discussion sections detailing the experimental work which was carried out. In the final chapter (Chapter 6), the experimental results are discussed more generally in relation to the persistence and control of the species on arable land.

Data presented in the chapters in the form of diagrams are tabulated in appendicies along with relevant statistics, and a full description of the growth analysis technique employed in Chapters 3 and 4 is also addended. Other appendices include climatic data and description of special equipment used in the investigation.

CHAPTER 1

REVIEW OF LITERATURE

1.1 INTRODUCTION

It is widely recognised amongst those people who work with, and and seek to control weeds, that an essential prerequisite is an appreciation of the biological characteristics of the plants concerned. Although *Achillea millefolium* L. is considered to be a weed in several countries (Holm, Pancho, Herberger and Plucknett, 1979) information concerning its biology is both exiguous and diffuse. The purpose of this section is twofold; first to set down in one place the biological information that is available and secondly to provide a basis for the experimental work of the following chapters.

1.2 NAME

Achillea millefolium L. is a member of the tribe Anthemideae, family Asteraceae (Compositae). The genus was named after Achilles who was said to have discovered the plants healing powers (Gray, 1950) whilst the species name refers to the finely dissected leaves. It is commonly known as yarrow or milfoil in Europe (Clapham, Tutin and Warburg, 1962), but the accepted common name in New Zealand is yarrow (Standard common names for weeds in New Zealand, 1969).

1.3 DESCRIPTION AND ACCOUNT OF VARIATION

The following description of *Achillea millefolium* L. is based on that of Clapham, Tutin and Warburg (1962). The plant is a perennial strongly scented, far-creeping rhizomatous herb with erect, usually simple, striate and unbranched stems up to 80 cm which may be clad in woolly hairs. Cauline leaves range from 1 - 15 cm, are lanceolate in outline, 2 - 3 times pinnate with linear subulate ultimate segments. Basal leaves are long stalked, up to 30 cm while cauline leaves are sessile often with 2 - 3 small axillary leaves (Figs. 2.4 and 2.5). Heads are from 4 - 6 mm in diameter and arranged in dense terminal corymbs (Fig. 2.2). The involucre is avoid with broad, brown or blackish,

scarious-margined bracts which are oblong, keeled and blunt, and sometimes glabrous. The ray florets, of which there are usually 5, are about one half as long as, and as broad as the involucre (Fig. 1.1). They are 3 - toothed at the apex and usually white in colour but forms with pink or reddish ray florets occur. Disk florets (Fig. 1.1) are white or cream-coloured. Cypselas are commonly 2 mm long and *en masse* are a shining greyish white and somewhat winged (Fig. 1.2). The plant is very variable in hairness and in the colour of the bracts.

Achillea millefolium L., a species considered native only in the Old World, forms part of the diverse *Achillea millefolium* species complex, members of which are spread widely throughout the temperate and subarctic regions of the Northern Hemisphere. In occupying such a diversity of climates, this complex has developed an exceptional number of climatic ecotypes. Clausen, Keck and Hiesey (1958) demonstrated the striking series of altitudinal and latitudinal climatic races that occur within the complex in western North America. Its forms occur without interruption across central California, in all its major environments, from the shores of the Pacific Ocean, over the hot, dry interior Great Valley to near the top of the Sierra Nevada at 3,400 m and eastward across the Great Basin. They also extend eastward to the Atlantic, southward to Mexico and up to Alaska and the tip of the Aleution Island chain. The North American complex as presently understood is comprised of a native transcontinental tetraploid (n = 18) group, which ranges from the Pacific to northeastern United States, and a native hexaploid (n = 27) group, confined to the Pacific coast. Both these groups show considerable morphological variation and ecotypic differentiation throughout their ranges (Clausen, Keck and Hiesey, 1940; 1958). Transplant studies carried out by Clausen *et al.* (1940; 1958) along a transect from the Pacific coast, across the Coastal Ranges and the Sierra Nevada, and controlled environment studies have shown that the various races are morphologically and physiologically adapted to their specific environments and are genetically distinct from one another. Maritime and dwarfish alpine races of similar appearance, as well as others adjusted to less extreme conditions exist in both the tetraploid and hexaploid groups. In 1952, Ehrendorfer reported that 170 known strains of the *Achillea millefolium* complex existed in North America. The European hexaploid, *Achillea millefolium* L. has been sparingly

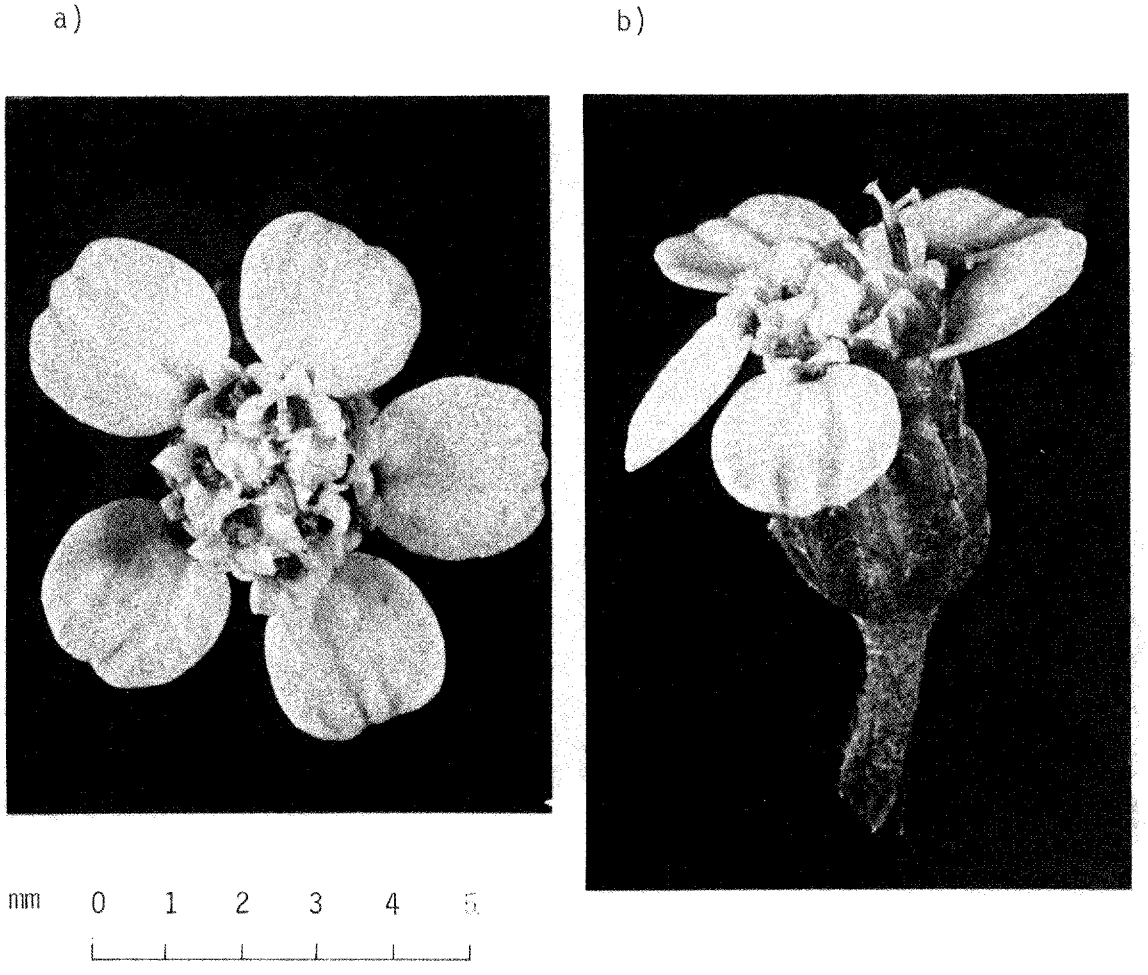


Figure 1.1 The flower head (capitulum) of *Achillea millefolium* L. a) Top view showing the five ray florets and a number of central disk florets; b) Side view showing involucral bracts and the separated stigmatic lobes protruding from the top of the extended anther cylinder of a disk floret.

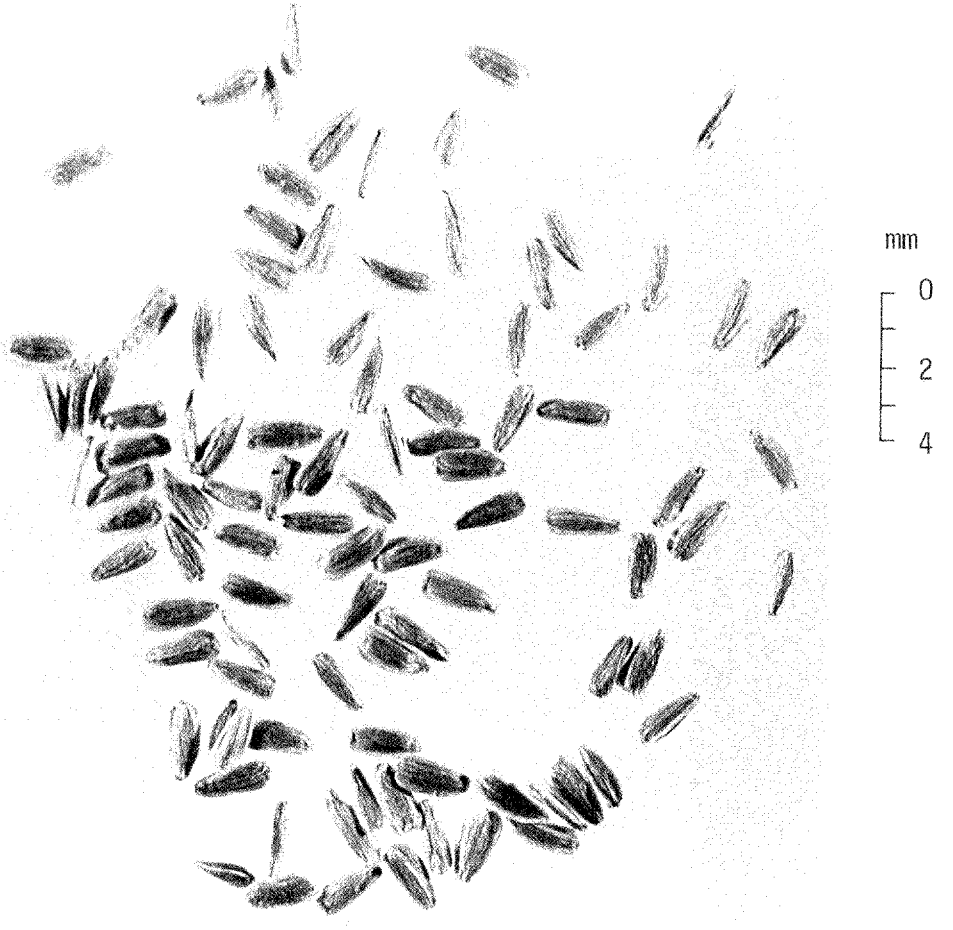


Figure 1.2 Cypselas of *Achillea millefolium* L.

introduced into Prince Edward Island, Nova Scotia and perhaps elsewhere along the Atlantic seaboard (Mulligan and Bassett, 1959). Although separated from the northern American tetra and hexaploids by trivial morphological characters of leaf cut and vesture (Clausen, Keck and Hiesey, 1958), the European hexaploid is considered to be a distinct species. Clausen, Keck and Hiesey (1940) were unable to successfully cross a Danish maritime form of *Achillea millefolium* L. and a coastal form of the *Achillea borealis californica* from California, each with 27 pairs of chromosomes.

Distinct ecotypes also occur within *Achillea millefolium* L. in Europe. Turesson (1930) found in transplant studies, marked differences in height between two ecotypes of Siberian origin, which often attained 1 m or more, and a Southern Sweden ecotype which never reached more than 50 cm. The Siberian and Scandinavian ecotypes were collected from the same latitude ($\simeq 55^{o}$ N) and showed no differences in earliness to flower. However, southern ecotypes from Munich, West Germany at 50^{o} N and from Vienna, Austria at 47^{o} N flowered later than the northern forms when grown together at Akarp, southern Sweden, indicating that the more northern ecotypes were physiologically adapted to ensure seed maturation during the relatively short northern summer. Clausen, Keck and Hiesey (1940) compared the growth of a maritime and woodland (inland) form of *Achillea millefolium* L. from Denmark in their uniform garden at Stanford, California. The maritime population produced stems ranging from 13 - 30 cm in length whereas the stems of the woodland form ranged from 26 - 65 cm. The maritime form, over a number of years, consistantly flowered one month earlier than the other and it was concluded that the two forms represented different ecotypes, being genetically distinct and adjusted to their natural environments.

The Danish maritime form of *Achillea millefolium* L. collected from a grass-covered, exposed sandy seashore on Zealand (55^{o} 17' N) proved to be winter and summer-active and early flowering when grown at Stanford in comparison to a Lapland form (within the arctic circle at 68^{o} 20' N) collected from a disturbed railway embankment which had characteristics of a subarctic ecotype. In the Stanford garden, this more northern form was winter-dormant but growth resumed quickly in the spring so that in some plants, flowers were present a month later (Clausen, Keck and Hiesey,

1958). Again, these forms were clearly different ecotypes, exhibiting genetically determined physiological mechanisms which would allow them to succeed in their natural environments.

Within New Zealand, there has been no detailed study of the considerable variation exhibited by the Achillea genus. Given (unpublished) considered most New Zealand specimens of yarrow to obviously fall within the *Achillea millefolium* L. species in a strict sense, but noted that several forms of uncertain affinity occur. Tall-growing, pink to deep red-flowered specimens with coarsely divided leaves, have been seen from Franz Josef, Milton, Greenstone, Central Canterbury Plains, Christchurch, Lake Ellesmere, Amberley and Bluff, which are probably referable to *Achillea distans* Waldst et. Kit, ex. Willd subspecies *tanacetifolia* Janchen, a member of the *Achillea millefolium* group. Another form, of which specimens have been collected from Banks Peninsula and North Canterbury have short stems, hairy involucral bracts and densely to moderately lanate leaves; possibly a member of the *Achillea nobilis* L. group. A further robust type with large leaves and involucres up to 7 x 5 mm has been collected from near Clyde in Otago and similar plants with grey leaves and conspicuous ovate ligules have been seen near Highbank, Canterbury, but these have not been matched with any known European species. Apart from *Achillea millefolium* L., two other species, *Achillea filipendulina* Lam. and *Achillea ptarmica* L. occasionally occur as garden escapes (Given unpublished).

The plant material used in the experiments reported in this thesis was grown from seeds and rhizome cuttings from populations occurring in arable fields in the vicinity of Lincoln College, Canterbury. A chromosome count revealed the material was hexaploid with 54 chromosomes.

1.4 ECONOMIC IMPORTANCE

1.4.1 Detrimental

In New Zealand *Achillea millefolium* L. is a common weed of waste places and roadsides in both Islands, but is commonest in the cultivated fields of the cereal growing areas where it is a serious weed, often growing so densely as to choke out cereal and other crops (Hilgendorf and Calder, 1952). Cockayne (1912) listed yarrow amongst the 50 common weed

seed impurities in farm seed and considered that the greatest factor in its spread was the use of impure seed. In a farmer-opinion survey relating to the seriousness of arable and pasture weeds in the South Island, yarrow was ranked 12th in a list of 15 major weeds (Cockayne, 1917). Connell (1930) noted yarrow as a 'twitchy' weed of arable land while Saxby (1944) regarded it as a bad weed on arable country on account of the competition it sets up with the sown crop and the labour that is required in eradicating it. Reynolds (1961) also considered it a serious weed of cropping land, being readily spread once established and McCaskill (1947) stated that it becomes the bane of cereal growers in regions of Canterbury where sown for sheep feed. It is a particular problem in perennial leguminous crops such as lucerne (*Medicago sativa* L.) (Matthews, 1975) white clover (*Trifolium repens* L.), seed crops (Bourdôt, White and Field, 1979) and other crops including peas (*Pisum sativa* L.), beans (*Phaseolus vulgaris* L.) and beets (*Beta vulgaris* L.). Bourdôt (unpublished) found that the seed yield of a white clover crop in Canterbury was reduced by 46% in the presence of a yarrow infestation with 104 flower stems m^{-2} while Allen (1967) and Wynn-Williams (1976) commented on the importance of elimination of yarrow from land to be sown to lucerne.

Yarrow increased and became the dominant weed in land continuously cropped with wheat (*Triticum aestivum* L.) in Hawkes Bay, New Zealand (Douglas, pers. comm.) and was noted as a local intruder of permanent autumn-sown wheat fields in Britain at Rothamsted (Warrington, 1958). In Russia, monocultures of rye (*Secale cereale* L.), oats (*Avena sativa* L.), clover (*Trifolium repens* L.) and flax (*Linum usitatissimum* L.) were associated with an increase in yarrow (Dospekhor, 1967). Mukula, Raatikainen, Lullukka and Raatikainen (1969) in a survey of spring cereal fields in Finland showed yarrow to be the second most frequent perennial weed; occurring in 69% of the fields. It was most abundant in spring cereals which followed leys and winter cereals, apparently escaping the plough.

In well managed pastures it is not considered as a serious weed but develops dominance in swards damaged by insects, herbicides or prolonged dry weather (Matthews, 1976) and increases in laxly managed pasture (Klappe, 1950). Konekamp (1964) considered yarrow to be a serious weed of

pastures in Germany, and Hay and Ouellette (1959) regarded it as a weed of pastures of eastern Canada. Habovstiak (1967; 1968; 1972; 1973) judged yarrow as a weed in Czechoslovakian pastures of the *Nardus stricta* type.

As a consequence of the production of aromatic compounds, yarrow has the ability to impart off-flavours to some agricultural products. Minor contamination of peppermint (*Mentha piperita*) with yarrow leads to tainting of the extracted oil and its down-grading (Fowlie, pers. comm.). The plant has also been implicated in the tainting of milk and its derivatives (Molfino, 1947; Singh and Kohli, 1956; Ministry of Agriculture, Fisheries and Food, 1968).

Yarrow is often regarded as a weed of lawns (Garthwaite, 1930), especially of fine turf (Greenfield, 1962) and putting greens (Sutton, 1950).

1.4.2 Beneficial

Achillea millefolium L. has been a favoured species for lawns and playing areas that are subject to heavy wear. Its solid, mat-forming rhizome/root system, and fine feathery leaves provide a dense, even and drought resistant turf that requires very little cutting (Reynolds, 1961). Although regarded as a weed in the finest turf, it blends well with turf grasses and is recommended sown at 14 g m^{-2} as a grass substitute. Its drought resistance makes it especially useful on 'light' soils (Greenfield, 1962). Sutton (1950) commented on the use of yarrow for golf course fairways, considering its ability to bear constant traffic and remain green long after grasses have lost their attractive appearance as important attributes.

In the early days of pastoral farming in New Zealand a small amount of yarrow seed was often included in hill country secondary and primary bush burn mixtures in both Islands, especially in the steeper and drier hill country (Macpherson, 1910; Cockayne, 1914; Levy, 1915; Cockayne, 1922; Ward, 1923; Levy, 1927; Tennent, 1935; Levy, 1936; Calder, 1944; Boot, 1946). Yarrow seed was also sown in Canterbury as sheep feed (McCaskill, 1947) but here it frequently became a serious weed in cereal crops. This species is now not greatly encouraged for agricultural use in New Zealand; though palatable and a good sheep feed (Cockayne, 1920 a,

b; Thomson, 1922; Monckton, 1927; Saxby, 1944) it is low producing and under modern farming techniques its presence hinders successful establishment of plants of superior potential (Reynolds, 1961). Yarrow was advocated for inclusion into seed mixtures for the renovation of mountain pastures in East Germany where it was also considered a useful remedy for stomach and intestinal troubles (Heeger, 1949). Mahlcke (1953) concluded that yarrow was a valuable component of ryegrass stands in dry localities in East Germany; although yarrow depressed the growth of ryegrass, due partly to its heavy uptake of soil nitrogen, when grown in mixture with ryegrass a 40% increase in pure protein and a 37% increase in crude protein occurred in the stand. Laity (1948) and Stapledon (1948) discussed the merits of yarrow and recommended its inclusion into pasture mixtures. Brynmor, Thompson, Oyenuga and Armstrong (1952) found yarrow contained a higher percentage by dry weight of calcium, phosphorus, potassium and magnesium than the grasses *Lolium perenne*, *Dactylis glomerata*, *phleum pratense* and *Cynosurus cristatus*. It was especially rich in potassium although of similar mineral efficiency to the grasses with regard to other elements. It was considered a distinctly useful component of grazing swards on soil types which normally grew poor swards. Bruggemann, Bronsch and Drepper (1960) did not substantiate these latter findings and found yarrow to have a high fibre but low nutrient content.

Some interest has been shown in the use of yarrow as a potential revegetation plant for eroded mountainous land in Canterbury. However, Dunbar (1971) did not rank the plant highly for this purpose as it was only moderately vigorous when sown on eroded slopes at Porters Pass, Craigieburn and Mt. Olympus and more over was a poor volunteer. On moderately eroded soils in northern Utah, Eastmond (1971) found *Achillea millefolium* L. was able to successfully initiate stabilizing associations and Loiseau (1975) demonstrated its suitability for establishing turf on soils denuded by skiing on the Plomb du Cantal Massif in France.

Not only is *Achillea millefolium* L. eaten readily by sheep, but is also palatable to horses and has been recommended as one of a number of desirable species for inclusion in seed mixtures for horse pasture (Archer, 1971). Poultry have also been shown to have a preference for yarrow as a grazing plant (Cowlishaw, 1960).

A considerable number of *Achilleas* are used as garden ornamentals (Synge, 1965) and several variants with flower colour ranging from deep red e.g. Fire King to the yellow of Flowers of Sulphur have been selected from *Achillea millefolium* L. (Synge, 1969).

Achillea millefolium L. has been employed for a great variety of medicinal purposes, its healing properties reputedly having been discovered by the Greek mythological war hero Achilles (Gray, 1950), who was said to have used it to staunch his soldiers bleeding wounds (Lowenfield and Back, 1974). It is possible that medicinal uses were made of the plant in prehistoric times because yarrow, along with other plants still prominent in ethnomedicine in Asia has been found at a 60,000 year old Neanderthal burial site in Shandidar, Iraq (Thomson, 1978). Yarrow is still officinal in Austria and Switzerland, being included in the pharmacopoeias as Herba Millefolii or Flores Millefolii (Clapham, Tutin and Warburg, 1962; Wagner, 1977). Yarrow has always been an important plant in the herbals and the following are some known properties. The plant has choleretic, antiinflammatory, antispasmodic, astringent and expectorant properties (Thomson, 1978); antibacterial, antihypertensive and spasmolytic qualities (Kaneko, pers. comm.); antiflatulent and diuretic characteristics (Lowenfield and Back, 1974); and fertility regulating ability (Laszlo, 1954). These attributes may provide explanations for various medicinal benefits apparently derived from the use of yarrow (Lowenfield and Back, 1974; Usher, 1974; Thomson, 1978). Although some of these properties are due to the presence of known compounds, none of these have been commercially extracted for use in pharmaceutical preparations, possibly because they show only weak activity (Kaneko, pers. comm.).

Despite its limitations and disuse in agriculture, the employment of yarrow on playing fields, and for stabilizing embankments has maintained a demand for its seed. Farmers in New Zealand have been tempted by high seed prices to save seed, often from natural weed infestations in white clover (*Trifolium repens* L.) seed crops, and frequently with indifferent results due to the uneveness of ripening, and the shattering of seeds from the ripe heads. Best harvesting conditions occur in an early season when seed ripens quickly and more evenly (Reynolds, 1961). A yield of 190 kg seed ha^{-1} would be considered good but the potential is

much higher than this (Bourdôt, unpublished).

1.4.3 Legislation

There has been no legislation concerning yarrow as a weed in New Zealand.

1.5 GEOGRAPHICAL DISTRIBUTION

Achillea millefolium L. is native to the British Isles and is widely distributed here and throughout Eurasia, extending from the Mediterranean region and northern Persia to the Arctic Circle and beyond (Clausen, Keck and Hiesey, 1958). It has been introduced into North America, Australia and New Zealand (Clapham, Tutin and Warburg, 1962). The plant has been recorded as a principle weed of Finland, Norway, New Zealand and Sweden; a common weed of Argentina, Australia, Canada, England, Germany, Hawaii, Iran, Soviet Union, Spain and U.S.A.; present as a weed in Chile and India and present in the floras of Afghanistan, Alaska and Poland (Holm, Pancho, Herberger and Plucknett, 1979). Within the New Zealand botanical region, *Achillea millefolium* L. is local north of 40^{o} latitude but becomes more frequent further south, especially in montane areas. In the South Island it is common up to at least 750 m, and is also present in the Kermadec Islands (Given, unpublished). It is common in waste places, roadsides, cultivated fields, grassland and streamsides, and is most frequent in the arable districts of Canterbury, Otago and Southland.

1.6 HABITAT

1.6.1 Climatic requirements

In Northern Europe *Achillea millefolium* L. inhabits a wide range of climatic regions. Clausen, Keck and Hiesey (1958) showed that the region occupied by a coastal Danish race had a January mean temperature of 0^{o} C and a July mean of 16^{o} C whereas the region inhabited by a Swedish Lapland race, 13^{o} farther north (within the arctic circle) had corresponding temperatures of -15 and 11.7^{o}. In New Zealand *Achillea millefolium* L. grows under a wide range of climatic conditions (Reynolds, 1961), ranging from the dryer and warmer climates of Canterbury with average annual rainfall from 600 - 800 mm and mean annual temperatures

from 10 - 12.5^{o} C to the cooler moister climate of Southland with average annual rainfall from 800 - 1200 mm and mean annual temperatures from 7.5 - 10^{o}.

1.6.2 Substratum

In England *Achillea millefolium* L. occurs on all but the poorest soils (Clapham, Tutin and Warburg, 1962) and in New Zealand it is also present under a wide range of soil fertility conditions (Reynolds, 1961). However it shows a preference for high fertility soils (Hanf, 1974), and Scott and Maunsell (1974) found it was more common on topdressed than on unimproved grassland and was most frequent on areas abundant in sheep faeces. Mukula, Raatikainen, Lalluka and Raatikainen (1969) in a survey of spring cereal fields in Finland found *Achillea millefolium* L. thrived on all kinds of soils from sand or fine sand to clay and to humus and peat, but it was most common on sandy soils. It tolerates a wide range of soil moisture conditions (Mukula *et al.*, 1969) but tends to be most abundant on dry soils (Andries, 1958; Lambert, 1963) while in New Zealand is widely distributed on lighter soils liable to summer drought (Matthews, 1976). It is a common plant on the dry chalk downs of England (Anderson, 1927) and shows a preference for neutral soils (Hanf, 1974).

1.6.3 Communities in which it occurs

Achillea millefolium L. occurs in a wide variety of habitats in New Zealand: spring and winter cereals (McCaskill, 1947), peas, beans, beets and clover seed crops (Bourdôt, White and Field, 1979) and perennial crops such as lucerne (Matthews, 1975) and peppermint (Bourdôt *et al.*, 1979). It is also common in pastures (Fenner, 1978), lawns (Garthwaite, 1930; Levy, 1931), roadsides and waste places (Matthews, 1975). The weed is most common in the cultivated fields of cereal growing regions (Hilgendorf and Calder, 1952) and may form dense stands in fields of white clover seed crops if not adequately controlled before sowing.

1.7 HISTORY

According to Thomson (1922) the presence of *Achillea millefolium* L. in New Zealand was first documented by Hooker in 1864 when he included it in his list of principal naturalised plants. The plant at this time had been observed growing in pastures in the Auckland area. It apparently

naturalised and spread rapidly for Kirk (1899) recorded it as common in both Islands and Cheeseman (1906) noted that it was not uncommon in the fields and on the roadsides of both Islands. Thomson (1922) cited it as very common in many parts of Otago. The species was probably introduced into New Zealand as an impurity in agricultural seed or intentionally, as a desirable pasture species. Certainly, its rapid spread through the agricultural regions of the country was largely assisted by the intentional inclusion of seed in pasture seed mixtures for sowing on land after primary and secondary bush burns in both Islands (Macpherson, 1910; Cockayne, 1914; Levy, 1927).

1.8 GROWTH AND DEVELOPMENT

1.8.1 Morphology

Yarrow is a persisting, creeping plant reaching 80 cm in height with a strong, much branched rhizome system. The first rhizomes develop from the woody, knotty axis of the primary shoot; later other rhizomes develop from nodular thickenings on the first formed ones (Korsmo, 1954). Not only do the rhizomes aid the exploitation of the immediate environment, but they also greatly assist the survival of the plant on cultivated land. Hilgendorf and Calder (1952) remarked on the difficulty experienced in bringing the entire rhizome system to the soil surface due to the brittleness of the rhizomes and Reynolds (1961) observed how the plant is readily spread by poor cultivation which breaks up the clumpy rhizome system and scatters the pieces, each of which is capable of establishing a new colony of the plant. Anderson (1927) found the rhizomes to be more or less horizontal in the soil and in loosely knit chalk soil they were more deeply buried than in compact soil.

Numerous fibrous roots are formed (Korsmo, 1954) which according to Laity (1948), penetrate deeply into the soil. Anderson (1927) in a study of the water economy of the English chalk flora showed yarrow was one of the more deeply rooting species on these dry calcareous soils with a maximum penetration of 22 cm while the maximum development of feeding roots occurred within the zone 5 cm - 11 cm. Root hairs were found to be frequent, well developed and evenly distributed.

Natural local populations of *Achillea* in western North America contain a wealth of different genotypes and it is common to see growing

under uniform conditions, a series of variable plants that originated from single mother plants in the wild (Ehrendorfer, 1952). This genetic variability affects morphological features such as height of stem, number of nodes, form and size of leaves, and degree of leaf cut as well as physiological characters. This variability of the *Achillea millefolium* complex in conjunction with a sturdiness and capacity to withstand rough treatment, the ability to adapt to a considerable range of conditions and become strongly modified is not only largely responsible for the wide distribution of the complex, but also equally accountable for the aggressive and often weedy nature of many races (Ehrendorfer, 1952). A high degree of variability also occurs in *Achillea millefolium* L. in New Zealand (Given, unpublished) and is undoubtedly an important factor in its persistance in such wide ranging habitats as permanent grassland and regularly cultivated fields.

1.8.2 Perennation

Raunkier (1934) described *Achillea millefolium* L. as a partial-rosette hemicryptophyte with subterranean stolons (rhizomes). Its resting buds and shoot apices are formed at the soil surface during the unfavourable season, thus affording the protection of a soil covering. In Britain, the plant produces new shoots in the autumn before the old stems die and these overwinter until the warmer weather in the following spring (Fryer and Makepeace, 1977).

1.8.3 Physiological data

Clausen, Keck and Hiesey (1958) in an attempt to elucidate the physiological adaptation of ecological races of *Achillea millefolium* L. from Europe subjected a Danish woodland ecotype and a more northern race from Lapland to variations of temperature and lighting in controlled environments. The Danish form flowered under an 8-hour day, under natural daylength and under continuous illumination but only when exposed to warm days of 26^{o} C combined with cool mild nights of 13 - 17^{o} C. It grew especially rapidly under 8 hours of light at 26^{o}C and 16 hours of supplemented light at 17^{o} C, flowering one month after the experiment started. Without supplemental lighting, flowering was delayed one month. At lower temperatures e.g. 17^{o} C day, 13^{o} night plus natural daylength, growth was very slow but healthy and no flowering occurred. The Lapland form was able to flower under 8 hour days at 26^{o} C and under 16 hour days at 17^{o} C

but when supplied with 16 hours of supplemental lighting at these same temperatures, flowering did not occur but the plants responded with increased rosette growth. Thus *Achillea millefolium* L. from northern latitudes apparently prospers at relatively high temperatures, developing with great rapidity under such conditions, especially when given additional light. Its forms flower in their native environment during the brief but warm summer, with long days and mild nights. Substantiating this prosperity under relatively high temperatures Mukula *et al.* (1969), in a survey of spring cereals in Finland over several seasons, found the average density of yarrow shoots in oats, barley and wheat was highest in a season subsequent to a fairly warm summer.

Turesson (1930) found appreciable differences in earliness to flower in forms of *Achillea millefolium* L. from central Europe and southern Sweden. The more southern central European forms from West Germany and Austria flowered consistently one week later than the Swedish form when grown together in Sweden, indicating that these races were physiologically adapted to their respective environments; the more northern forms flowering earlier to allow seed maturation in the shorter northern summer.

Clausen, Keck and Hiesey (1940) considered the *Achilleas* to be plants of sunny habitats. It was found that plants of the western North American hexaploid and tetraploid species were weak and seldom flowered when shaded but as soon as placed in sunny conditions started to bloom. No information is available on the tolerance of the European hexaploid, *Achillea millefolium* L., to shading.

The majority of buds on the rhizomes of undisturbed *Achillea millefolium* L. remain dormant due to strong apical dominance (Bourdôt *et al.*, 1979), and regardless of the time of year, buds on single-node rhizome pieces showed activity exceeding 90%. Thus there was no period of innate bud dormancy in the rhizomes of the population studied. Hensen (1969), similarly was unable to detect a pronounced period of bud dormancy in the rhizomes of *Achillea millefolium* L. in Britain although the regenerative ability of 3 cm rhizome fragments appeared to be lower during the winter months.

1.8.4 Phenology

The seasonal activity of growth in the *Achilleas* varies with race

and environmental conditions. Clausen, Keck and Hiesey (1958) found that the native *Achilleas* at a site 22 km in from the ocean on the west coast of North America were not prevented from growing during the winter months and indeed used this cool winter rainy season for active vegetative growth. The dry summer and autumns however checked growth entirely unless irrigation was applied. These authors also found that two hexaploid Danish races were continuously active when transplanted in California but a sub-arctic race from Lapland was distinctly winter-dormant here despite the suitability of conditions for the other races. Thus these ecotypes appeared genetically adapted to their native environments. *Achillea millefolium* L. in Britain, remains dormant during the cold winter months until conditions warm in the following spring (Fryer and Makepeace, 1977). Contrary to this, Bourdôt, White and Field (1979) found *Achillea millefolium* L. to be a vigorous autumn/winter-grower in Canterbury, forming considerable amounts of rhizome during this period. In a Department of Agriculture reply to A.H. Rowe (1924) it was suggested the autumn growth of yarrow was greater than that of lucerne and hence likely to succeed at the expense of the latter. In Britain, new shoots are formed in the autumn (Fryer and Makepeace, 1977) but in Canterbury, most rhizome tips do not emerge to form new shoots until the spring following active winter rhizome growth (Bourdôt, White and Field, 1979).

Flowering occurs during the months of November through to March in Canterbury while fruiting occurs from January with peak capitulum weight in late March, and seeds are still being shed from the capitula as late as July (Bourdôt, White and Field, 1979). However, Thomson (1922) recorded flowering as beginning much later in February and continuing until March. Flowering begins in late spring in Britain and similarly continues for about five months (Fryer and Makepeace, 1977), with fruiting occurring over a six-month period from early summer (Bostock and Benton, 1979). The flower stems die back in the autumn and winter (Fryer and Makepeace, 1977; Bourdôt, White and Field, 1979).

Freshly shed seeds germinate in copious quantities on bare ground after rain during the autumn in Canterbury (Bourdôt, White and Field, 1979) and also during the summer on irrigated cropping land (Bourdôt, unpublished). Yaskonis and Bandzaitene (1970) found seeds sown in late autumn in Russia did not germinate until the following spring whereas Zelencuk (1956) showed germ-

ination occurred throughout the year on a peaty meadow. In Canterbury seedlings establishing from autumn-germinating seeds grow very slowly during the winter months (in contrast to the rapid vegetative growth of established, rhizomatous plants), until the following spring when new rhizomes and flower stems are formed (Bourdôt, White and Field, 1979).

1.8.5 Mycorrhiza

Anderson (1927) reported the association of fungal filaments, although few in number, with the roots of *Achillea millefolium* L. on the English chalk soils.

1.9 REPRODUCTION

1.9.1 Floral biology

In *Achillea millefolium* L. the arrangement of the heads or capitula in a corymbose manner gives a continuous flat surface to the conflorescence (Leppik, 1977) with adjacent ray florets overlapping one another. Not only is the plant thus rendered conspicuous, but a single visitor may pollinate numerous florets (Knuth, 1908). Insects can pass from one head to another without having to fly using the contiguous ligulate ray-florets as bridges. A wide range of insects act as pollinators of *Achillea millefolium* L.. Thomson (1922) listed six species of flies which are pollinators in Europe and members of the orders, Diptera, Coleoptera, Hymenoptera, Lepidoptera and Hemiptera have been recorded on the flowers (Knuth, 1908). Nectar is produced and secreted by a ring of glands surrounding the style at the base of the narrow tubular corolla. It accumulates and rises up into the wider part of the corolla tube where it is protected from rain (Leppik, 1977) and becomes available to visiting insects. Magnarelli, Anderson and Thorne (1979) discussed the nectar-feeding patterns of salt marsh Tabanidae (Diptera) on yarrow and other species of coastal salt marshes of eastern North America. They concluded that the presence of common nectar sugars and pollen grains in these deer flies suggests an important association between these insects and the host plants. Externally, deer flies were sometimes heavily covered with composite and grass pollen around the head, prothoracic regions and on the legs, and thus undoubtedly served as vectors for pollen.

Weijer (1952) stated that anatomically the flowers are ideal for self pollination and Knuth (1908) further discussed this point. However Clausen, Keck and Hiesey (1940), in an attempt to cross a plant of the hexaploid European species, *Achillea millefolium* L. from Denmark with a plant of the coastal form of *Achillea borealis californica* from America (also a hexaploid) found that not only were they cross-incompatible, and thus distinct species, but both were also highly self-incompatible. Furthermore, they found no seeds were produced after isolation or after emasculation followed by cross-pollination and therefore concluded that these Achilleas were not apomictic. Thus *Achillea millefolium* L. is an obligatory outbreeding species, with barriers to selfing which nullify any advantage resulting from the gynomonoecious habit of the capitulum (Knuth, 1908) and its functionally protogynous nature (Burtt, 1977).

1.9.2 Seed production and dispersal

Based on a mean of 25.5 cypselas capitulum^{-1}, Bourdôt, White and Field (1979) estimated that 2,800 cypselas stem^{-1} could be formed in a pure stand of yarrow, giving approximately 900,000 cypselas m^{-2} and that an individual plant free from competition, in its first season could be expected to produce 60,000 cypselas. Bostock and Benton (1978) found that approximately 23.3 ovules capitulum^{-1} were formed. Reynolds (1961) commented on the plants free-seeding ability and Hughes (1915) remarked of yarrow and some other perennial weeds, " ..... although not supposed to produce as many seeds each time as annuals, yet leave far too many descendants behind". Hanf (1974) estimated that 3,000 to 4,000 seeds plant^{-1} could be produced.

In a study of the effects of density on growth and reproduction, Deschenes (1974) found seed production unit area^{-1} to at first increase with increasing density but then to decline markedly at high densities when only a minority of plants produced seed. At low densities, about 500 seeds were produced reproducing plant^{-1}, but at high density only 4 seeds reproducing plant^{-1} were formed.

The small, one-seeded fruit (cypsela) was estimated to have a mean dry weight of 0.158 g by Bostock (1978), and similarly Bourdôt, White and Field (1979) recorded a mean dry weight of 0.166 g. Because a pappus is lacking, Bostock (1978) considered the seed to have no aerodynamic

efficiency in comparison with the plumed species; *Cirsium arvense, Taraxacum officinale* and *Tussilago farfara*. However, Reynolds (1961) noted that owing to their small size, the seeds were easily windblown for short distances and suggested that wide distribution may occur in sheep's wool. Clausen, Keck and Hiesey (1958) suggested that wind transport of the seeds was important in aiding the blending and shuffling of populations of *Achilleas* in western North America. Although there is no pappus, the flattened, winged habit of the fruit would appear to give it a degree of aerodynamic efficiency.

1.9.3 Viability of seed and germination

The seed of yarrow has been shown to have a high level of viability when freshly shed and exhibits a considerable degree of longevity. Robocker (1977) found that under optimum conditions, in petri dishes, 99% of freshly harvested seed germinated and after nine years dry storage, more than 41% germination occurred. It was considered that the ability of seeds to survive for extended periods may explain the distribution of yarrow from areas of high rainfall to semi-arid regions. Simulating more natural seed storage conditions, Bostock (1978) stored yarrow seed, and those of four other perennial composites, in soil at 27^{0} C and 80% relative humidity, to induce rapid ageing. Yarrow had the highest initial viability, with 96.9% germination of fresh seed, and retained viability better under the conditions of storage than the other species (*Artemisia vulgaris, Cirsium arvense, Taraxacum officinale* and *Tussilago farfara*). Bostock found that 92% of the initial viability remained after six months of soil storage; conditional dormancy was maintained to a high degree and thus there was little loss of seed through fatal germination in the soil. It was inferred from this data, that seed longevity of yarrow was high in comparison with the other species. Yaskonis and Bandzaitene (1970) also found yarrow seed to have a high degree of viability and obtained 92% germination under optimum conditions. Seed incorporated into soil had a lower germination than surface-sown seed, indicating the presence of enforced dormancy. These high initial viabilities and germination percentages support the similar finding of Bourdôt, White and Field (1979).

Robocker (1977) demonstrated the existence of a short period of after-ripening in the seeds; freshly harvested seed germinated 64%, but

this increased to 96% after two months. A minor trend toward periodicity of germination occurred in one and two year old, dry-stored seeds, with highest germination in summer (99.4%) and lowest germination in winter (92.6%). This periodicity was lost in nine year old seed and no practical importance was placed upon it.

Both light and temperature have a significant effect on the germination of the seeds. Yaskonis *et al.* (1970) found maximum germination (92%) could be obtained with temperature alternating from 18 to 21^{o} C and that light had a positive influence. Bostock (1978) also demonstrated a positive light requirement for germination. Robocker (1977) secured maximum germination of 99% with alternating temperatures of 15 and 25^{o} C with concurrent dark and light periods. In the International Rules for Seed Testing (ISTA, 1976) the requirement of light and temperature alternation is recognised in the recommendation for maximum germination of 16 hours darkness at 20^{o} C alternating with 8 hours light at 30^{o} C.

Dorph-Peterson (1925) described yarrow as having germination spread over a period of months when sown on bare ground and as germinating partly after fruiting and partly in the following spring. Such observations are explicable in terms of the breaking of conditional dormancy of at least three types of seed with different requirements for germination (Bostock, 1978).

Oomes and Elberse (1976) found that yarrow seed had a rapid water uptake relative to other grassland species and this was associated with better germination on drier substrates. The findings of Bostock (1978) suggest also that yarrow seed has some tolerance of relatively dry substrates for germination, but germination was maximal under conditions of ample moisture.

Bostock (1978) concluded that yarrow seeds were well adapted to intermittently available situations for seedling establishment. Although the seeds have no obvious means of spatial dispersal, they do have dispersal in time by virtue of considerable longevity and complex dormancy which maximise the chance of establishment success. Being small and plumeless, they may be easily incorporated into the soil where they may remain until sensing an open situation at the surface, in for example, the grassland habitats in which the species commonly occurs.

1.9.4 Vegetative reproduction

Yarrow, in common with the other *Achilleas*, forms a system of underground stems or rhizomes from which regeneration can occur (Clausen, Keck and Hiesey, 1958), and although the reproductive potential of this system on arable land has been alluded to (Saxby, 1944; Hilgendorf and Calder, 1952; and Reynolds, 1961) specific information is lacking. Bostock and Benton (1978) related the reproductive strategy of yarrow, and four other perennial composites to the theory of r and K selection (Gadgil and Solbrig, 1972). They found that yarrow allocated 2.7% of its net production to seed and 26.0% to rhizome and concluded that this species was by far the most K - strategic of the five species studied. It was considered that this distinction corresponded to the likely degree of disturbance in the natural habitat, and accorded with the predictions of r and K selection; yarrow occurs typically in pastures and waysides where density-dependent mortality would be high, and therefore tends to allocate a greater proportion of its resources to non-reproductive activities (exploitive rhizome system) in comparison to the species living in environments imposing high density - independent mortality, e.g. *Tussilago farfara*. The authors noted however, that the vegetative reproductive capacity of yarrow depends partly on the environmental conditions. Both the amount of disturbance likely in the habitat (e.g. grassland *versus* cultivated field) and the susceptibility of the propagules to such disturbance should be taken into account when estimating how far the average field reproductive capacities will approach the maximum potential values (when every bud forms a new plant). Bourdôt, White and Field (1979) found that after one season of growth from a planting density of 38, 10 cm rhizome fragments m^{-2} almost 6 tonnes of new rhizome dry matter ha^{-1} had been produced in the absence of competition from other species. Rhizome extension has been recorded at rates ranging from 7 to 20 cm $year^{-1}$ (Salisbury, 1942).

1.10 POPULATION DYNAMICS

A population of *Achillea millefolium* L. may extend over several hectares, or along several kilometers of roadway. Bourdôt, White and Field (1979) reported a density of 320 flower stems m^{-2} in an established stand with a mean of 109 capitula $stem^{-1}$. The mean number of seeds

produced capitulum^{-1} was 25.5 giving an approximate seed output of 2780 stem^{-1} and 900,000 m^{-2}. Bostock and Benton (1978) found there was a mean of 149.4 capitula stem^{-1} in a wild population and 23.3 ovules capitulum^{-1}. Only 55.4% of these ovules developed and 11.2% of the seed was destroyed by predators so that only 11.1 seeds capitulum^{-1} were dispersed, i.e. approximately 1,660 seeds stem^{-1}. Details of rhizome production are not reported in the literature although Bostock and Benton (1978) revealed that plants growing in 14-cm pots for 2 years had produced 201 nodes plant^{-1} on a total length of rhizome of 218 cm plant^{-1}. It has been shown by Bourdôt *et al.* (1979) that a large proportion of the buds at these nodes are capable of forming new plants when released from the influence of the apical bud by fragmentation of the rhizome and consequently, the degree of disturbance of the rhizomes will determine how far the field vegetative reproductive capacities approach the maximum potential value.

Achillea millefolium L. exhibits considerable plasticity in response to increased density. Intrapsecific competition in this species was observed through a plastic response of yield at low to medium densities and through both plasticity and mortality at high density (Deschenes, 1974). Optimum shoot and root yields per unit area were obtained at a density of 96 seed-grown plants m^{-2} above which yields unit area^{-1} remained constant. At 868 plants m^{-2} 22% mortality occurred. Seed production unit area^{-1} increased with increased density up to 288 plants m^{-2}, then decreased markedly at higher densities. This response of seed yield to increasing density was associated with a decline in the percentage of reproducing individuals and a decline in the number of seeds reproducing individual^{-1}. Thus it was concluded that the yarrow population was regulated by individual plasticity, mortality and limited seed production. The competitive success of yarrow in a mixed population depends on the other species present. Mukula *et al.* (1969) reported that yarrow was more abundant in oats and wheat than in barley, indicating that barley was the stronger competitor.

1.11 RESPONSE TO HERBICIDES

Achillea millefolium L. is controlled by only a few herbicides. In waste places, picloram can be used and gives effective control. Picloram applied to the soil and to foliage early in the growing season controlled *Achillea millefolium* L. (Montgomery, 1966) and when applied in a mixture

with 2,4 -D (65 g picloram and 240 g 2,4 -D litre^{-1}) at 1, 2 and 3 litres ha^{-1} gave complete control (Williams, 1966). 2, 3, 6 -TBA at 22 to 33 kg ha^{-1} gives similar results to picloram (Matthews, 1975).

A late application (early winter) of both 2, 4 -D amine and 2, 4 -D ester at 15, 30 and 45 litres ha^{-1}, although removing the clovers, eradicated *Achillea millefolium* L. from a permanent pasture (Svensson, 1959), whereas applications at the same rates in spring and summer had little effect. Jakobsons (1974) found that mecoprop and dichlorprop at 4.0 kg ha^{-1} both controlled the plant in pasture. A mixture of 2, 4, 5 -T and 240 g of picloram litre^{-1} applied at 3 litres ha^{-1} as an overall spray to a permanent pasture controlled the plant, but because this herbicide was toxic to *Trifolium repens* and several other non-graminaceous herbage species, only spot applications to pasture were recommended (Richter, 1966).

Some herbicides and mixtures have been shown to control *Achillea millefolium* L. in turf. A single application of dicamba at 0.56 kg ha^{-1} in early autumn gave good control in a grass lawn (Research Station, Canada Department of Agriculture, Saanichton, 1970). Ahrens, Lukens and Olson (1962) achieved control in turf with dicamba and a mixture of 0.28 kg of dicamba and 1.12 kg of mecoprop ha^{-1} applied as a split application with a 2 to 4 week interval also controlled the plant in turf (Canada, Agriculture Canada, Research Station, Sidney, 1976). When turf containing *Achillea millefolium* L. was treated with a split application of mecoprop at 1.68 kg ha^{-1} in the late spring with 2 weeks between sprayings, control of the weed was apparently achieved (Canada, Canada Department of Agriculture, Research Station, Sidney, 1973). Dicamba at 0.56 kg ha^{-1} applied simiarly gave more effective early control but recovery was better than with the mecoprop treatments. 2, 4, 5 -TP has also given control of *Achillea millefolium* L. in lawn (Davis and Bandarenko, 1960).

Glyphosate gave good control of *Achillea millefolium* L. when applied in the spring at 1.5 kg ha^{-1} to a dense stand that had grown undisturbed in lupin (*Lupinus spp.*) stubble during the preceeding autumn and winter. Control was greater when the glyphosate was applied to 8-week regrowth following rotary-cultivation but a greater percentage control was achieved in the previous treatment (Bourdôt and Butler, unpublished). Glyphosate is the most suitable herbicide prior to no-tillage cropping because good control is achieved without residual soil activity (Matthews, 1976). Other

chemicals which apparently give some control of *Achillea millefolium* L. are simazine, dinoseb and diphenamid in strawberries (Collins and Everett, 1965) and dichlobenil in bush fruit (Jones, 1969).

1.12 RESPONSE TO OTHER HUMAN MANIPULATIONS

Although *Achillea millefolium* L. grows under a wide range of soil fertility conditions, it has been classified as a high fertility weed since it persists on high fertility soils in spite of the presence of high-producing desirable species (Hay and Ouellette, 1959; Reynolds, 1961). A sward consisting of *Anthoxanthum odoratum*, *Carex panicea*, *Sieglingia decumbens* and *Nardus stricta* in Czechoslovakia became dominated by *Achillea millefolium* L. along with *Festuca pratensis*, *Poa trivalis* and *P. pratensis* after four annual dressings of fertiliser containing nitrogen, phosphorous and potassium (Haken, 1968). Similarly, Habovstiak (1967, 1968, 1973) in attempts to improve pastures with a high proportion of *Nardus stricta*, found *Achillea millefolium* L. increased substantially when nitrogenous fertilisers were applied; three annual dressings of 150 kg N ha^{-1} resulted in the third year in a complete take-over by *Achillea millefolium* L. (Habovstiak, 1972). In New Zealand, Scott and Maunsell (1974) showed yarrow was more abundant on oversown and topdressed tussock grassland than on undeveloped areas, and furthermore, was most abundant on sheep camps and on sites plentiful in faeces. However other workers have shown that desirable species can be favoured at the expense of yarrow by increasing the fertility of the soil (Peters and Lowance, 1973) and by controlled grazing and mowing in conjunction with fertilisation (Konekamp, 1964).

The response of *Achillea millefolium* L. to cultivations has not been reported in the literature. However some general recommendations involving cultivations in control programmes have been made which suggest they can be detrimental to the survival of the plant. Connell (1930) made reference to the weakening effect of summer cultivations and suggested they should be augmented by sowing immediately, a dense, quick-growing crop to suppress regenerating plants. This method of control was also advised by Saxby (1944) and Hilgendorf and Calder (1952), the latter authors recommending oats (*Avena sativa*) sown with tares (*Vicia sativa*) as a good, rapid-growing smothering crop. The effect of repeated cultivations is probably partly the result of exhaustion of rhizome food reserves due to the growth of

shoots stimulated by fragmentation, and their subsequent destruction (Bourdôt, White and Field, 1979). Hilgendorf and Calder (1952) stated that the plant is difficult to eradicate by the ordinary methods of twitch control (dragging rhizomes to the soil surface, allowing them to desiccate and then harrowing them into heaps to be burnt) because the rhizomes are too brittle to allow them to be brought to the surface. However, Reynolds (1961) suggested early autumn ploughing, followed by cross-grubbing would leave the soil in large clods which would readily dry out, and be easily broken down to allow the rhizomes to be eaten by sheep. Hilgendorf and Calder (1952) also advocated using sheep to add to the effects of cultivation while Allen (pers. comm.) commented on the plants apparent intolerance of autumn cultivations.

Although *Achillea millefolium* L. is highly palatible to sheep, it is also resistant to grazing (Steen, 1954). Fuellman and Graber (1938) showed that overgrazing associated with depletion of fertility and drought on the permanent *Poa pratensis* - dominant grasslands of south western Wisconsin, lead to a great increase in weeds, including yarrow. Matthews (1975) commented about the plants tendency to increase under close grazing and mowing, its resistance to grazing, and ability to recover (Reynolds, 1961) apparently being augmented by the reduction in the stature and hence competitive ability of associated grasses. Yarrow did not compete with tall-growing vegetation (Matthews, 1975). Contrary to these findings, yarrow has been found to increase along with grasses upon the exclusion of sheep from previously grazed pasture (Nature Conservancy, 1962; Welsh and Rawes, 1964). It would seem that the recovery and/or increase of yarrow in a sward of other species after grazing has ceased must depend upon the abundance of these species, their rate of recovery and competitive ability. Laycock and Harniss (1974) revealed yarrow to be highly susceptible to trampling by sheep.

Soil compaction has been shown to have an influence upon the rhizome system. In loosely knit soils, rhizomes penetrate relatively deeply (Anderson, 1927) and the plant increases rapidly (Saxby, 1944). In more compact soils, such as under pasture, the rhizome system is usually displaced to quite shallow depths (Saxby, 1944; Reynolds, 1961).

Hvidsten (1953) found yarrow seed survived in silage whereas the

seeds of 16 other weed species were all killed.

1.13 RESPONSE TO PARASITES

1.13.1 Nematodes

Several species of nematodes have been found to attack *Achillea millefolium* L. Crossman and Christie (1937) noted that *Achillea millefolium* L. was attacked by the plant-infesting nematode, *Anguina millefolii* in the U.S.A. A new species, the yarrow cyst nematode (*Heterodera achilleae*) was found to heavily attack *Achillea millefolium* L. in a potato growing area in Yugoslavia but did not attack the potato (Morgan and Klindic, 1973). This species of nematode was recorded as infesting the roots of *Achillea millefolium* L. (Morgon and Klindic, 1973), which was subsequently found to be the primary host (Klindic and Petrovic, 1975). Only a few other plant species, also from the Asteraceae family showed host value. *Heterodera achilleae* was reported as widely distributed in Yugoslavia (Klindic and Petrovic, 1975).

1.13.2 Leaf miners

Two species of leaf miners have been recorded on *Achillea millefolium* L. *Phytomyza achilleae* is parasitic on the plant in Switzerland (Hering, 1931) and another species, *P. matricariae* feeds on representatives of *Achillea, Chrysanthemum, Matricaria* and *Tenacetum* in Canada (Sehgal, 1971). Spencer (1976) when reviewing the *Phytomyza* species did not record *P. achilleae* or *P. matricariae* as being present in New Zealand.

1.13.3 Other insects

The thrip, *Haplothrips angusticornis* Pr. is locally common and widely distributed in Great Britain in the flowers of *Achillea millefolium* L. In Holland and England, the aphids, *Pleiotrichophorus duponti* and *Macrosiphoniella usquertensis* have been found feeding on *Achillea millefolium* L. and *Dactynotus tanaceticola* was found on the plant in England (Hille, 1935). *Chrysura boharti* (Hymenoptera) was recorded in the flowers of *Achillea* spp. in New Zealand and the parasitic larva of *Galeruca tanaceti* were found on the leaves of *Achillea millefolium* L. in France (Laboissiere, 1934).

1.13.4 Plants

Kraft (1979) reported *Orobanche purpurea* growing on *Achillea millefolium* L. in Sweden while *O. minor* has been recorded as a parasite of the plant in Canterbury (Bourdôt, unpublished).

CHAPTER 2

STRUCTURE OF THE AERIAL SHOOT, RHIZOME AND ROOT SYSTEMS

2.1 INTRODUCTION

While the structure and functioning of the flowers of *Achillea millefolium* L. have been reported in the literature (see Review of Literature, Chapter 1), there has been no report concerning the structure of the vegetative reproductive system. Because some aspects of the biology of the rhizome system are dealt with in this study, a brief description of its formation and structure is presented here, the information having been derived from observations and measurements made throughout the course of this work. Some aspects of the structure of the aerial shoot system are also presented.

2.2 AERIAL SHOOT SYSTEM

The primary aerial axis formed by seedlings, plants regenerating from rhizome fragments and by shoot systems developing at the apex of an emerged rhizome, initially consists of up to 30 closely spaced nodes, each with a leaf and an axillary bud. When interference from neighbouring plants is absent, for example in widely spaced seedlings or in single axes growing from spaced rhizome fragments, several axillary buds close to the soil often grow out plagiotropically at first and then, after a few centimetres of growth, turn upward forming decumbent basal second order axes (Fig. 2.1). Up to 20 of these basal branches have been produced by isolated plants growing from seed (Bourdôt, White and Field, 1969). Interference from neighbouring plants or shoots of the same or other species often prevents the formation of these basal axes, and the primary axis then branches from axillary buds only in the upper region forming distal second order axes (Fig. 2.1). Distal axes are also formed in the upper axils of the basal second order axes (Fig. 2.1). These distal branches are always reproductive and contribute to the size and complexity of the conflorescence (Fig. 2.2). The buds in axils of leaves in the middle regions of the ascending aerial axes either remain dormant or form small fascles of leaves.

The general form of the leaves of *Achillea millefolium* L. has been

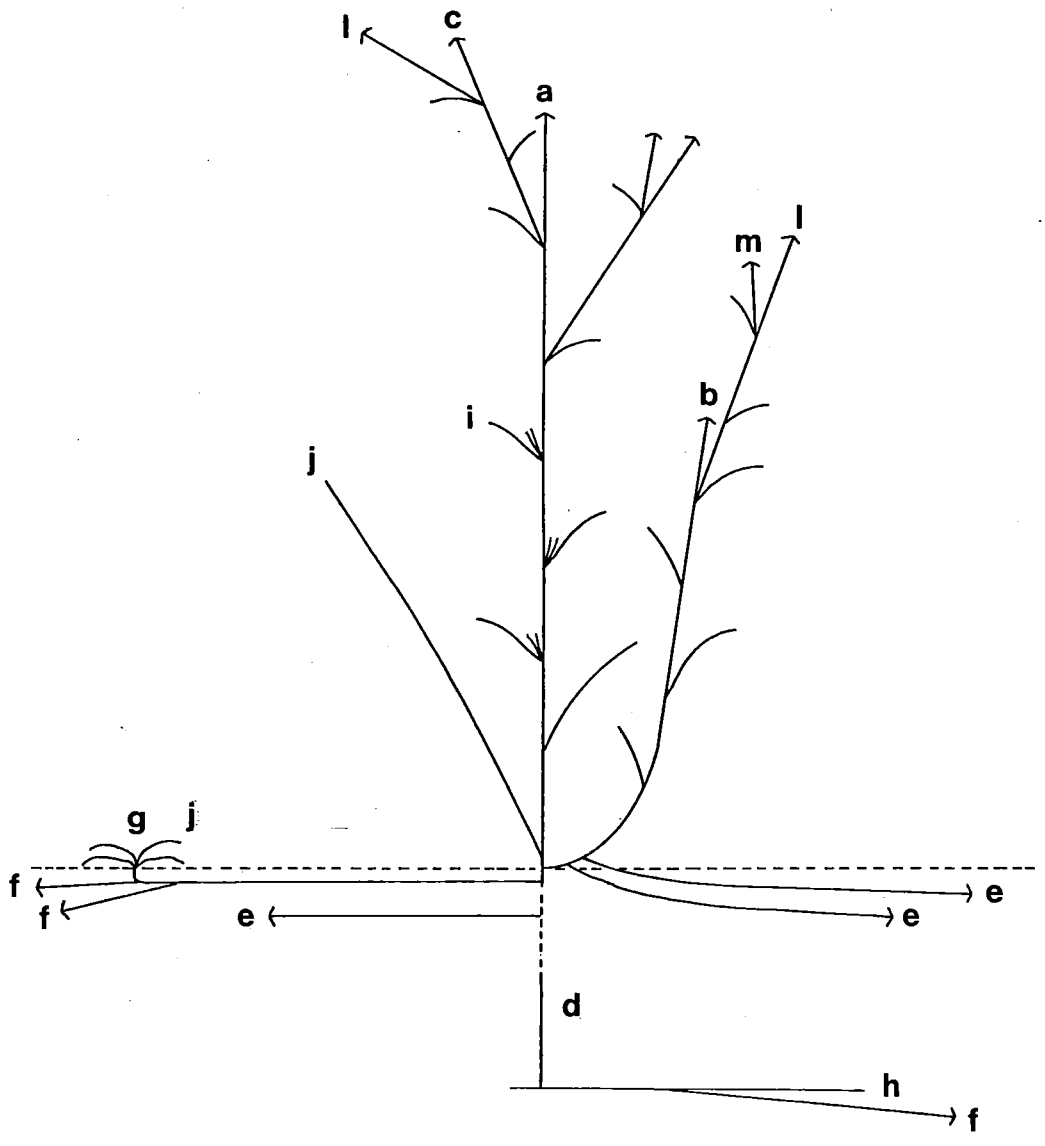


Figure 2.1 Schematic diagram of a mature plant of *Achillea millefolium* L. established from a rhizome fragment/seed. **a**, primary axis; **b**, basal second order axis; **c**, distal second order axis; **d**, vertical subterranean shoot; **e**, primary rhizome; **f**, secondary rhizome; **g**, emerged rhizome apex; **h**, rhizome fragment; **i**, cauline leaf; **j**, rosette leaf (basal); **l**, third order axis; **m**, fourth order axis.

Figure 2.2 A conflorescence of *Achillea millefolium* L.

outlined in the preceding literature review. However, the material utilised in this study showed considerable variation in leaf size, thickness, degree of dissection, presence of petioles, width and orientation of pinnae depending upon position on the plant and the local environment. The leaves of rosette plants growing in open, high-light environments such as cultivated fields were noticeably thicker than in closed-stand environments, almost succulent and quite brittle. These leaves ranged up to 17 cm in length and had no petiole. Pinnae were sually arranged in the same horizontal plane as the midrib and tended to be quite broad (Fig. 2.3). In dense stands or clumps of plants, or when other species were in close association, the rosette leaves of vegetative shoots and the basal leaves of flowering stems had distinct petioles, often as long as one third of the leaf length (Fig. 2.4). The leaves in these situations grew nearly vertically upward, commonly reaching 30 cm in length, with the pinnae surfaces still horizontal but now at a steep angle (up to 90^{o}) to the ascending midrib. The pinnae of these leaves were generally further apart (up to 15 mm), much narrower and thinner than in the open situation and were also feathery to touch.

The 16 or 17 cauline leaves varied in length from 20 - 30 cm near the base of the stem to 1 cm near its apex (Fig. 2.5). These leaves were sessile and ranged from 3 pinnatisect near the base of the stem to 1 pinnatisect near the apex, with the leaves of the middle regions clasping the stem. Pinnae were generally more closely spaced (1 - 5 mm) than on leaves originating at ground level in a stand.

2.3 SUBTERRANEAN SYSTEMS

2.3.1 Rhizomes

The plants of *Achillea millefolium* L. used in this study formed a system of horizontal underground stems or rhizomes. Sometimes the middle region of the rhizomes looped up out of the soil, apparently as a response to an impediment to extension growth, such as compacted soil. This phenomenon was recorded in plants growing naturally in the field and in experimental potted plants. However, these underground stems generally remained below the soil surface and consisted of a series of elongated internodes separated at varying intervals by nodes at which buds and

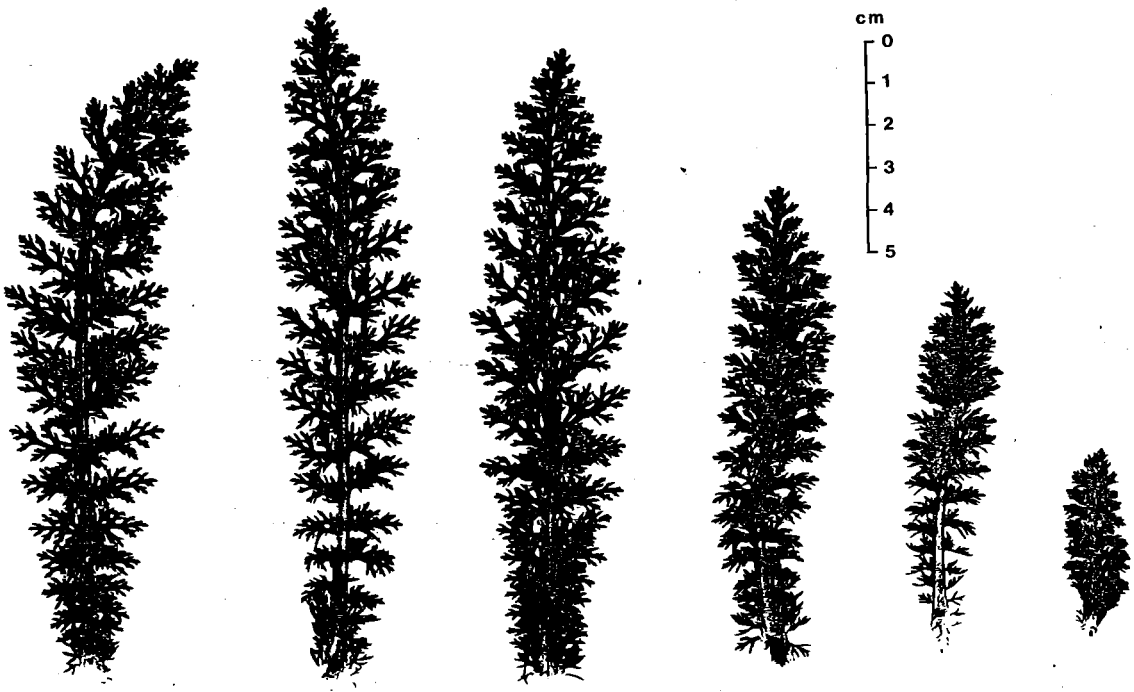


Figure 2.3 Leaves of rosette-plants of *Achillea millefolium* L. from an open situation.

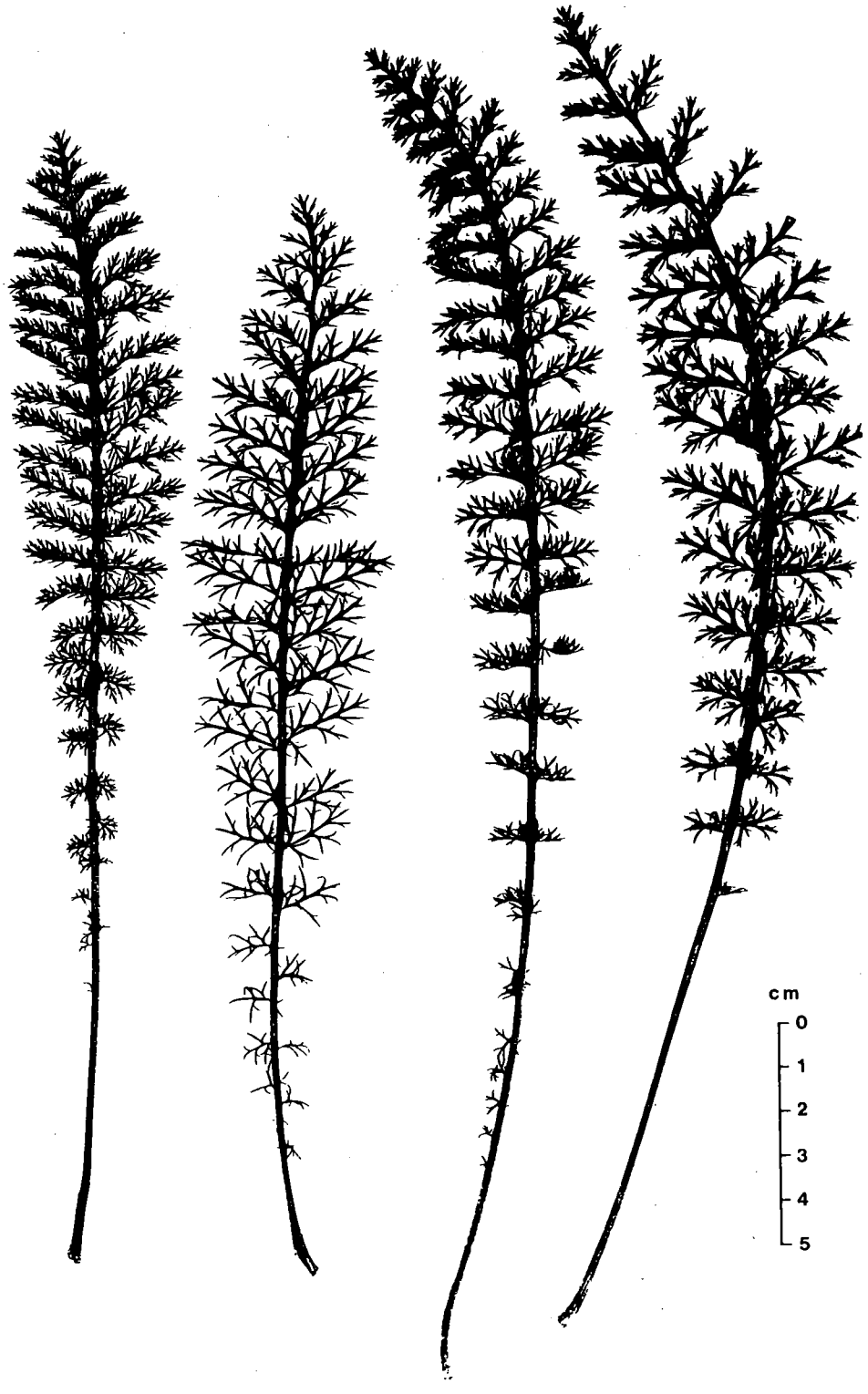
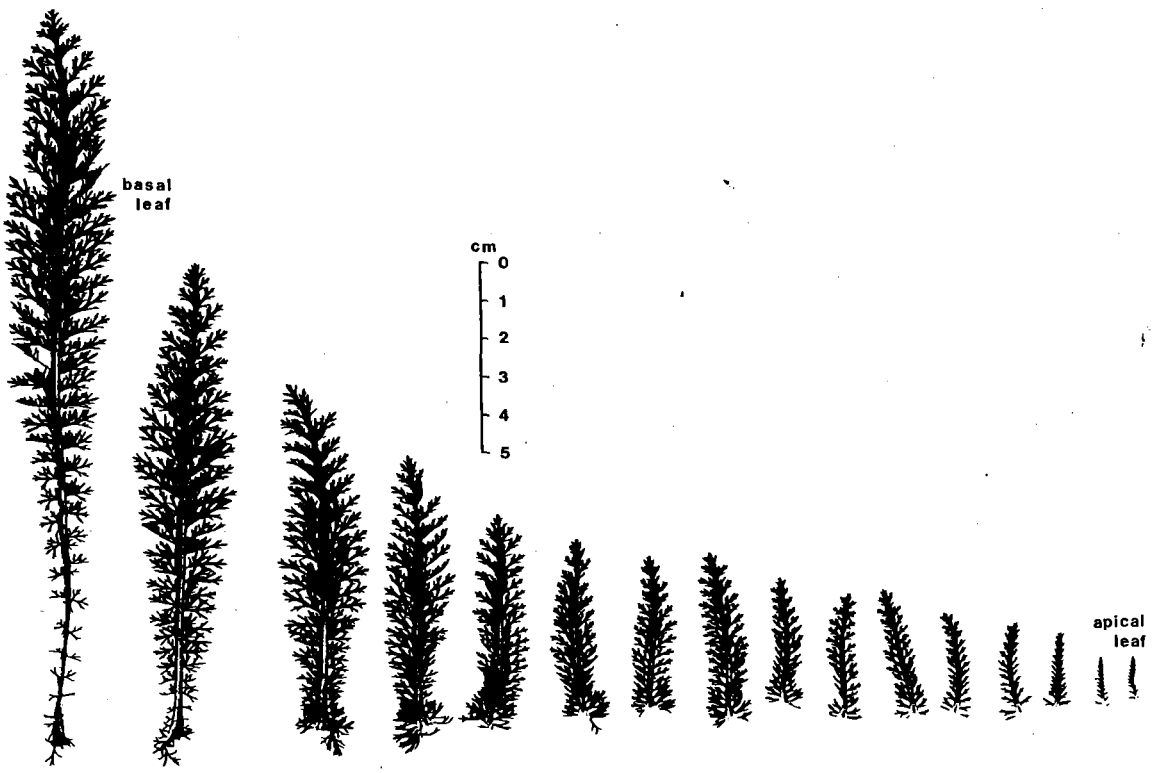


Figure 2.4 Leaves originating from the base of a dense stand of *Achillea millefolium* L.



igure 2.5 The variation in leaf habit with position on the flowering stem.

scale leaves were produced (Fig. 2.6). They therefore fitted the usually accepted definition of a rhizome given by Lawerence (1958). Confusion does however exist in the botanical definitions relating to creeping plant organs, and this is reflected in the variety of terms to which the rhizome system has been referred: subterranean stolon (Raunkier, 1934), creeping root stock (Allan, 1940; Matthews, 1975), runner (Korsmo, 1954), stolon (Clapham, Tutin and Warburg, 1962; Parham and Healy, 1976), rhizome (Bostock and Benton, 1979), and quite incorrectly, creeping root (Hilgendorf and Calder, 1952).

At the apex of actively elongating rhizomes, a series of spirally arranged scale leaves are formed which are imbricated and thus protect the growing apex from the abrasion of soil particles (Fig. 2.6). These scale leaves, along with developing axillary buds are successively separated by internode extension as the rhizome grows through the soil. Initially the scale leaves are quite fleshy but as they age they begin to dry and shrivel to form thin, brown, closely appressed coverings through which the bud often protrudes and which, on old rhizomes, are frequently absent, having been sloughed off in the soil. Korsmo (1954) has discussed and illustrated the anatomy of the rhizome and its apex.

Rhizomes varied in diameter from only 1 to 2 mm up to 5 to 6 mm. Rhizome diameter generally increased with age probably as a result of secondary thickening, (Korsmo, 1954) but often very young rhizomes were 6 mm in diameter. In the young actively elongating region behind the apex, the rhizome tissue was extremely brittle allowing the rhizome to break upon the slightest pressure, especially when fully turgid. This property was remarked upon by Hilgendorf and Calder (1952) when they attributed the difficulty of eradicating yarrow from arable land by cultural methods to this phenomenon.

Primary rhizomes originated at two locations in seedlings. The first rhizomes were initiated extravaginally from the lowest axillary buds on the main axis while other primary rhizomes were formed from buds in the lower leaf axils of basal second order axes (Fig. 2.1). In plants regenerating from buried rhizome fragments, primary rhizomes, as well as being initiated in the same locations as in seedlings, were also formed at nodes on the vertical subterranean shoots (Fig. 2.1 and Fig. 2.6). Secondary rhizomes are formed on the primary rhizomes and on

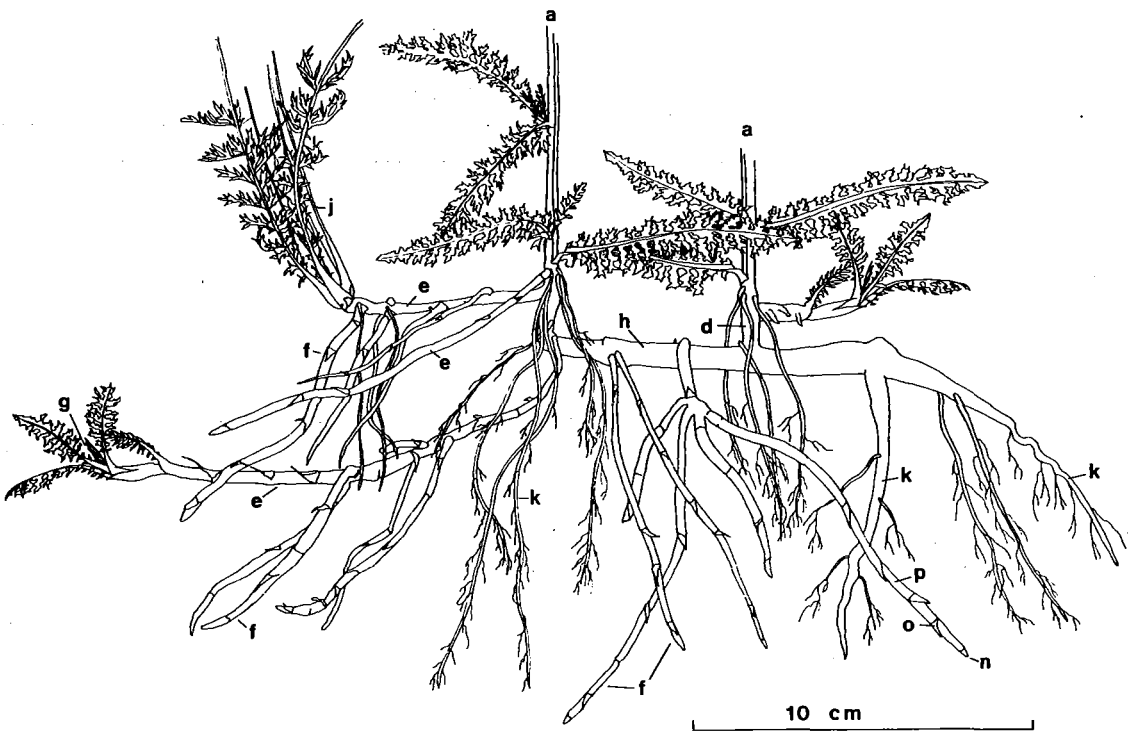


Figure 2.6 A simplified drawing of the rhizome system of a plant of *Achillea millefolium* L. in autumn having established from a 10 cm rhizome fragment planted in the previous spring. **a**, primary axis; **d**, vertical subterranean shoot; **e**, primary rhizome; **f**, secondary rhizome; **g**, emerged rhizome apex; **h**, rhizome fragment; **j**, rosette leaf (basal); **k**, adventitious root; **n**, apex of elongating rhizome; **o**, scale leaf; **p**, internode.

buried regenerating fragments from activated axillary buds (Fig. 2.6). This aspect of the development of rhizomes is fully discussed in Chapter 5.

2.3.2 Roots

The germinating seedling produces initially a single seminal root (Fig. 2.7). This axis branches throughout its length, forming up to fourth order laterals and probably higher orders. In young vegetative rosette plants, the seminal axis may vary from 2 mm in diameter in its upper regions to less than 0.5 mm near the apex. First order laterals are commonly less than 1 mm in diameter. Root hairs were most abundant on the highest order laterals and decreased in abundance back toward the seminal axis on which few were present. Large numbers of nodal root axes were formed from the base of the seedling's main axis as this increased in diameter (Fig. 2.7). These axes were commonly formed both below and above the nodes from which primary rhizomes and basal second order aerial axes were formed and thus sometimes originated at or just above soil level. These root axes were very similar to the seminal axis with regard to branching and root hair formation and made up the bulk of the root system of plants establishing from seed (Fig. 2.7).

Actively elongating rhizomes attached to the parent plant and without emerged apices seldom formed roots. However upon the emergence of the apex from the soil and the formation of a new aerial shoot system, roots were soon formed adventitiously from the apical internodes of the upturned rhizome (Fig. 2.6). These roots were in all respects similar to the nodal axes formed on seedling plants and were similarly formed, apparently randomly along the internodes of this transitional zone of the emerged rhizome. They formed the root systems of the new daughter plants. Occasionally adventitious roots did arise from all of the internodes of an emerged rhizome but this was rare. This pattern of rhizome-root development contrasts sharply with that of other rhizomatous plants e.g. couch (*Agropyron repens*) which forms adventitious roots throughout its rhizome system, and only at the nodes.

Plants regenerating from rhizome fragments characteristically produced adventitious roots at two locations. Initially several roots were formed at the basal end of the rhizome fragments after emergence

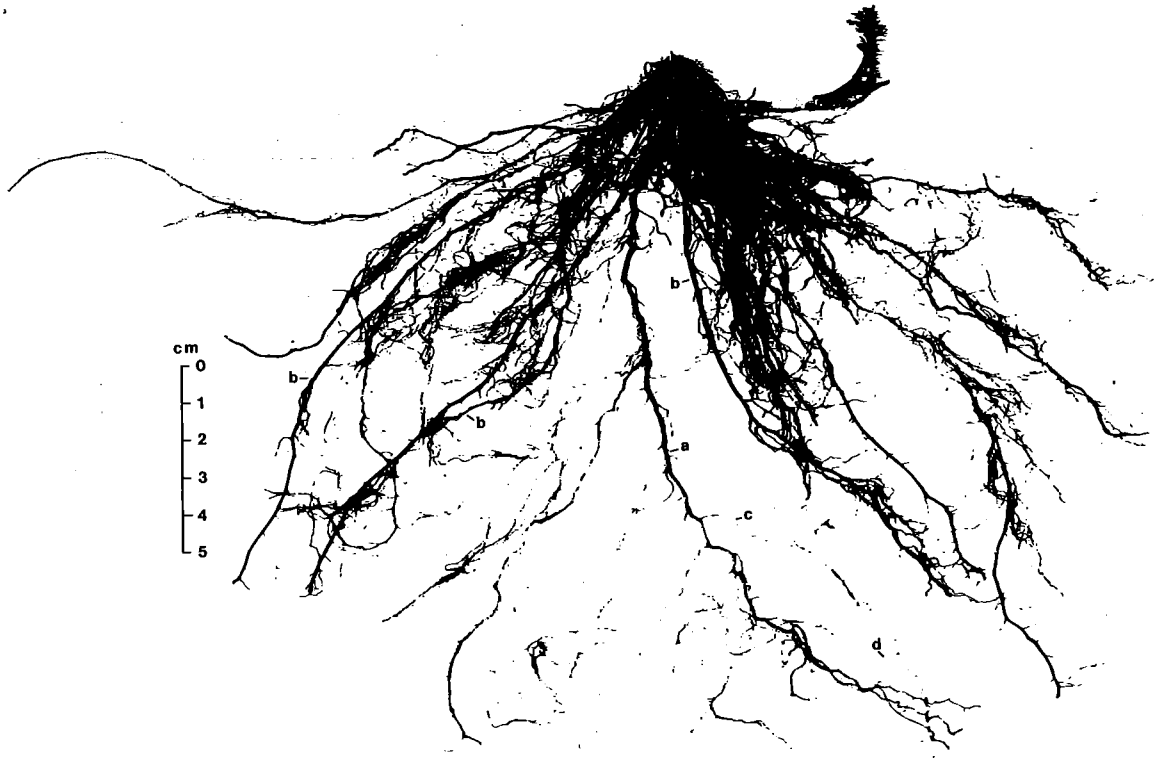


Figure 2.7 The root system of *Achillea millefolium* in the first season of growth after establishing from a seed. **a**, seminal axis; **b**, nodal axis; **c**, first order lateral; **d**, second order lateral.

of the vertical subterranean shoots (Fig. 2.6). These branched several times in the manner previously described but their main axes commonly become very stout as in a tap root. Some time later, more roots were initiated from the internodes of the emerged vertical shoots. These roots were similar to the nodal axes formed on seedlings and similarly formed the main part of the new plant's root system.

CHAPTER 3

THE ADAPTABILITY OF YARROW SEEDLINGS TO SHADE

3.1 INTRODUCTION

It is widely known that different plant species establish and grow in an exceedingly wide variety of light environments. Some species appear to be facultative 'shade' plants, for example, *Impatiens parviflora* an herbaceous annual, introduced into Britain, forms natural communities both in the open and in the deep shade of deciduous woodlands where light intensities range from 30 to 60% of full daylight during the period after leaf fall, to 0.2 to 5.0% when the leaf canopy is fully expanded (Coombe, 1965). This species produces dry matter as efficiently at 24% of full daylight as it does in full daylight (Evans and Hughes, 1961). Other species seem to be obligate 'shade' plants, for example *Geum urbanum* and *Solanum dulcamara*, both occurring naturally in shady habitats, produce dry matter most efficiently at light intensities considerably below full daylight (Blackman and Wilson, 1951 b), and when exposed to higher intensities show a reduction in efficiency. Still others are 'sun' plants, growing most efficiently under high light conditions, for example: *Fagopyrum esculentum*, *Trifolium subterraneum*, *Helianthus annuus* (Blackman and Wilson, 1951 b), *T. hybridum*, *T. pratense*, *T. repens* and *Medicago sativa* (Blackman and Black, 1959).

The relative abilities of different species to tolerate shade may be explained by (1), morphological adaptations involving change in the size of the photosynthetic system, affecting its ability to intercept light and causing change in its efficiency; (2), physiological or metabolic adaptations effecting changes in the efficiency of the photosynthetic system, involving both photosynthetic and respiratory adaptations. Growth analysis has provided a means of grossly separating the two so that their relative contributions may be assessed. This is so because the relative growth rate (RGR, the increase of plant material per unit of material present per unit time) is the product of the leaf area ratio (LAR, the ratio of the assimilatory area per unit of plant material present) and the net assimilation rate (NAR, the increase of plant material per unit of assimilatory area per unit of time). Furthermore, the LAR or leafiness,

can be assessed in terms of its two components; specific leaf area (SLA, the ratio of leaf area to leaf weight) and leaf weight ratio (LWR, the ratio of the leaf weight to total plant weight). The SLA is thus a measure of the spatial distribution or expansion of the leaf tissue, and the LWR is the proportion of the total plant material allocated to leaf tissue. The NAR is also a composite function representing the excess of the rate of photosynthesis of leaves over the rate of respiration of the whole plant expressed in terms of leaf area (Watson and Hayashi, 1964).

For a wide range of species LAR and NAR are inversely related, LAR increasing and NAR decreasing as shading is increased, for example; *Helianthus annuus*, *Fagopyrum esculentum*, *Trifolium subterraneum*, *Tropaeolium majus*, *Lycopersicum esculentum*, *Vicia faba*, *Pisum sativum*, *Hordeum vulgare*, *Solanum dulcamara* and *Geum urbanum* (Blackman and Wilson, 1951 a, b), *Fraxinus excelsior* (Wardle, 1959), *Impatiens parviflora* (Hughes and Evans, 1962; Coombe, 1965; Hughes, 1965 a, b, c;) *Quercus petraea* (Jarvis, 1964), *Lycopersicum esculentum* (Hurd and Thornley, 1974) *Crotalaria juncea* and *C. sericea* (Pandey and Sinha, 1977). The response of these two growth functions to the level of shading necessarily determines the response of the RGR. Blackman and Wilson (1951 a, b) found that both the NAR and LAR were linearly related to the logarithm of the relative light intensity over the range from 100 to 13% of full daylight and by multiplying the two functions together, derived the response of the RGR. Furthermore, it was considered that accurate determination of the light compensation points of species could be obtained by extrapolating the fitted linear regressions to the light axis, assuming the continuance of linearity. On the basis of these studies it was concluded that plants could not be defined as 'sun' or 'shade' species either on the basis of the response of NAR to reduced light intensity, nor in terms of varying compensation points. The mean values of the compensation points ranged from 6 to 9% of full daylight for eight species (including 'sun' and 'shade' plants), whilst for *Vicia faba* and *Hordeum vulgare* somewhat higher figures were obtained - 14 and 18% of daylight. However, the response of the LAR to reduced light varied greatly between the species, leading to the suggestion that 'shade' plants are best defined as those for which the LAR increases rapidly upon

shading from a low level in full daylight; the converse was propounded for 'sun' plants (Blackman and Wilson, 1951 b). As a consequence of the greater adaptive response of LAR with shading in 'shade' species, the RGR was buffered against the declining NAR and hence remained high or indeed, in some instances, reached a maximum at light intensities considerably below full daylight. For example, the RGR of *Geum urbanum* reached a maximum at 54% full daylight and declined at higher and lower intensities (Blackman and Wilson, 1951 b), whereas the maximum RGR of *Trifolium repens* was predicted to occur at 185% full daylight (Blackman and Black, 1959). This adaptive response of the LAR to shading has also been demonstrated in *Crotalaria spp.* (Pandey and Sinha, 1977), while other workers have resolved it into its components, SLA and LWR. The adaptability of the LAR in many cases is almost entirely the result of plasticity of the SLA (Evans and Hughes, 1961; Jarvis, 1964; Grime, 1965; Hughes, 1965 a; Loach, 1970; Hurd and Thornley, 1974; Packham and Willis, 1977), whereas plants appear to be able to alter the proportion of total dry matter in leaf tissue within only narrow limits (Evans and Hughes, 1961, Coombe, 1965), although Jarvis (1964) showed the LWR of *Quercus petraea* increased with shading while LWR was reduced steeply with shading in the 'sun' species, *Helianthus annuus* and *Vicia faba* (Kuroiwa, Hiroi, Takada and Monsi, 1964).

Hughes (1959) has discussed the anatomical changes in shaded leaves of *Impatiens parviflora* and showed that shade and sun leaves are fundamentally similar in meristematic activity and that the difference in the structure at maturity of leaves in full daylight compared to those at 7% full daylight was that the latter were only 37% as thick as the former and were considerably more expanded with a less well developed palisade layer and a diffuse spongy mesophyll. Packham and Willis (1977) showed that the shade leaves of *Oxalis acetosella*, another well known 'shade' plant, were more than twice as broad as sun leaves and considered that bulging outer walls of epidermal cells and the funnel-cells of the palisade layer caused the light to converge towards the base of the palisade cells, hence illuminating the chloroplasts more brightly than they otherwise would be.

In contrast to the conclusions of Blackman and Wilson (1951 b), the results of other workers suggest that the response of NAR may vary

considerably between species. For example, Evans and Hughes (1961), in a comparison of the shade tolerance of *Impatiens parviflora* and *Helianthus annuus* found the NAR of *H. annuus* at 12% daylight was reduced to 17% of its full-daylight value whereas the NAR of *Impatiens parviflora* was only reduced to 33%. The LAR of *H. annuus* was increased to 207% of its full daylight value while the LAR of *I. parviflora* was increased to 239%. These responses resulted in the RGR of *H. annuus* at 12% daylight being only 35% of its full-daylight value while the RGR of *I. parviflora* was 79% of its value in full daylight. It is clear that the difference in the responses of the RGRs was mainly due to variation in the responses of the NARs. This evidence suggests that the response of the NAR to shading may be just as important in differentiating between 'sun' and 'shade' plants, on the basis of the stability of RGR under reduced light, as the LAR appears to be.

Although there is general agreement that the remarkable adaptability of LAR which occurs in many plants when they are shaded, may explain the relative shade tolerance of species, there is much less understanding of the ecological significance of the light compensation point. It has been argued that 'shade' plants are likely to display lower compensation points than 'sun' plants (Bohning and Burnside, 1956), hence allowing the continuation of growth at light intensities below the minimum required by shade intolerant species. Thus Evans (1976) contrasted the exceedingly low compensation point of *Impatiens parviflora* (0.2 to 1.0% of daylight) as determined by Hughes (1965 a) in controlled conditions with that determined for the shade intolerant species, *Hordeum vulgare* and *Vicia faba* (10% of daylight) by Blackman and Wilson (1951 a). However the estimate of the compensation point is probably more accurate for *I. parviflora* as only a short extrapolation was required, but may be doubtful for *H. vulgare* and *V. faba* because long extrapolations of linear NAR regressions were required, necessitating unjustified assumptions about the response of NAR near the compensation point. Further investigations by Blackman and Black (1959) using screens outside, but with light intensities down to 5.5% of full daylight indeed showed that for several species, including *Helianthus annuus*, *Medicago sativa*, *Trifolium hybridum*, *T. repens*, *Lolium multiflorum* and *Phaseolus multi-*

florus, the response of NAR to the logarithm of the relative light intensity was curvilinear as a result of there being little change in NAR with increase in light intensity at low light intensities (around 10% full daylight). This sigmoidal response of NAR was considered ecologically meaningful because such species would be better able to survive periods of intense shading than those in which the response is logarithmic. In this respect *Vicia faba* and *Lolium maritimus* were classed as intolerant of deep shade. Similarly, Jarvis (1964) found the NAR of seedling *Quercus petraea* was curvilinear on the logarithm of the relative light intensity, there being little effect of changing intensity at low levels compared to the more rapid response at higher intensities. Coombe (1965) showed that the NAR of *Impatiens parviflora* also was not linear on the logarithm of the relative light intensity at low light levels. It is clear that in any of these cases of curvilinearity at low intensities, extrapolation of lines fitted to responses of NAR at relatively high intensities would be likely to over-estimate the value of the compensation point for light. Such problems in estimating the compensation point, in conjunction with its sensitivity to environmental factors other than light, for example, temperature (Grime, 1965) prevent a statement being made on its possible ecological significance.

In the continued search for an explanation of the tolerance to shade displayed by herbaceous forest-annuals and tree seedlings which survive under very low light intensities, and to allow recognition of physiological characteristics of species and ecotypes which could be used as reliable indices of shade tolerance, the photosynthetic and respiratory components of NAR have been investigated separately. Shade tolerant species have inherently a low respiration rate and low RGR and therefore may exhibit greater carbohydrate economy at light intensities near or below the compensation point (Grime, 1965; Loach, 1967). In comparison, shade intolerant species tend to have inherently higher respiration rates. In support of this concept, Mahmoud and Grime (1974) demonstrated that the shade tolerant *Deschampsia flexuosa* and the intolerant *Agrostis tenius* and *Festuca ovina*, although having very similar compensation points, differed markedly in their negative RGRs. The relative rate of loss of dry matter at light intensities below the compensation point was greater

in *A. tenuis* and *A. ovina* than in the tolerant *D. flexuosa*, thus leading to faster utilisation of reserves in the former two species and an inability to withstand light intensities below the compensation point for prolonged periods. Similarly, Loach (1970) demonstrated that the intolerance of low light displayed by *Populus tremuloides* was due to low assimilatory efficiency as a result of a high respiration rate.

The photosynthetic apparatus shows considerable adaptability to light intensity. In a comparison of 'shade' and 'sun' ecotypes of *solidago virgaurea*, Bjorkman and Holmgren (1963) demonstrated that 'shade' ecotypes had a higher photochemical capacity than 'sun' ecotypes as indicated by the steeper initial slope of the rate/intensity curve of apparent photosynthesis. This data implied that the shade ecotypes were able to use weak light more efficiently than 'sun' ecotypes, whereas populations from exposed habitats had higher rates of apparent photosynthesis at light saturation intensities, implying that they could utilise high light more efficiently. Similarly, Bohning and Burnside (1956) showed 'sun' species to have higher rates of photosynthesis than 'shade' species at saturation levels and also that saturation levels occurred at about 25% daylight for 'sun' species and 10% for 'shade' species. Chlorophyll content and chloroplast numbers have been shown to be lower in 'shade' plants when exposed to high light (Bjorkman and Holmgren, 1963; Jarvis, 1964; Packham and Willis, 1977). This may be caused by destruction of chloroplasts in 'shade' adapted ecotypes under high light (Bjorkman and Holmgren, 1963) and partially explain the inability of 'shade' ecotypes of *Solidago virgaurea* to adjust to high light and the reduction in the NAR and RGR of the shade tolerant *Quercus petraea* seedlings at light intensities above 66% full daylight (Jarvis, 1964). The data available provide evidence that species and ecotypes of habitats with contrasting light intensities differ in their photosynthetic properties in an adaptive manner which could prevent their establishment and survival in other light environments.

The evidence seems to suggest that shade intolerant species tend to have both high photosynthetic rates and high respiratory rates which would result in the high RGRs necessary for successful colonisation of exposed habitats (Grime, 1965). Loach (1967) found that shade tolerant

tree seedlings were most clearly differentiated in terms of maximum photosynthetic and respiration rates; intolerant species had higher rates of photosynthesis at saturating intensities and higher rates of dark respiration. High rates of photosynthesis, associated with high RGRs in intolerant species do not confer shade tolerance probably because they are offset by the accompanying high rates of respiration (Grime, 1965). It has been argued that the high rates of metabolism, including both photosynthesis and respiration which are apparently a requirement for successful colonization of exposed habitats prevent such species from establishing and surviving in shaded environments where productivity is low and carbohydrate economy may be of high importance (Grime, 1965).

Failure of seedlings in shade is almost invariably associated with fungal attack (Grime, 1965). There is some evidence that shade intolerant species may be predisposed to fungal attack due to their lower sugar content as a result of high respiration in the shade (Packham and Willis, 1977).

Grime and Jeffrey (1965) considered that a distinction can be drawn between shade tolerance and shade avoidance. Forest floor species need to be shade tolerant as shade avoidance is clearly not possible, but grassland species tend to show both avoidance and tolerance (Fenner, 1978). The facility with which a plant escapes shade low down in a canopy by height increase is related to the amount of storage material in the seed or vegetative propagule, and the number and nature of extension sites on the shoot. Initial height growth in shade is marked in seedlings of species occurring in dense grassland, for example, *Arrhenatherum elatius*, *Plantago lanceolata*, but is negligible in herbaceous species which are restricted to low turf and bare soil such as *Arenaria serpyllifolia*, *Hieracium pillosela* and in trees which are pioneers of abandoned arable land such as *Betula populifolia*, *B. lenta* and *Rhus glabra* (Grime and Jeffrey, 1965 In many 'sun' plants, height increase under shade either does not occur or etiolation is so great that mechanical collapse occurs due to the lack

of strengthening tissues. Fungal attack often then occurs on such collapsed plants.

The relative shade tolerance and or presence of shade avoidance mechanisms are undoubtedly of major ecological importance in determining the distribution and performance of species in both natural and man-made environments such as crops and pastures. The inability of pasture legumes, for example *Trifolium repens*, to adapt to shaded conditions, and hence their high light requirement (Blackman and Black, 1959), may be largely responsible for their disappearance from ungrazed or uncut grassland and their difficulty of establishment under cover crops (Black, 1957). The competitive ability of plants is governed in part by the efficiency with which they utilise light. Black, Chen and Brown (1969) classified many agricultural weeds and crop plants as photosynthetically efficient; continuing to fix increasing amounts of Co_2 as light intensity is increased to full daylight. These plants could thus be classed as 'sun' plants and as such would probably be unable to adapt to reduced light intensities. Consequently, yield reductions in either the crop or weed could be caused by one species shading the other, the relative effects in either direction being primarily dependent upon the relative times of emergence, density and growth habit of the plants. Rapid shading by crop canopies has been reported to suppress the growth and development of weeds, with the rate of canopy formation varying markedly with crop species (Keely and Thullen, 1978) and planting density (Herbert, 1977).

Fenner (1978) showed that colonising and closed-turf species could be separated on the basis of their tolerance to reduced light. Closed-turf species reacted appropriately to artificial shading by displaying avoidance mechanisms such as elongation of petioles, for example, *Trifolium pratense*, *Rumex acetosa* or whole leaves, *Plantago lanceolata*, *Achillea millefolium*, *Hypochaeris radicata* whereas the colonising species either did not adapt morphologically, for example, *Capsella bursa-pastoris*, *Senecio vulgaris* or etiolated to the extent that mechanical collapse occurred, *Spergularia arvensis* and *Stellaria media*. The closed-turf species also showed tolerance to reduced light intensity, maintaining their RGRs at relatively high levels compared to the colonising species, when shaded to 6.8% full daylight.

Yarrow is highly productive in open fertile sites but also persists in waste places, in roadside communities of tall-growing ruderals, in pastures and under cereal crops such as barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*) where light intensities may be reduced to very low levels. In all of these situations the plant displays an extremely high degree of variation, especially with regard to leaf form and the presence and vigour of flowering and rhizome formation. The plant is however absent from permanently shaded environments such as under trees or hedges; Clausen, Keck and Hiesey (1940) described the plants in the *Achillea* genus as those of sunny habitats, seldom flowering and weak in the shade. As already mentioned, Fenner (1978) showed yarrow to have a considerable capacity to tolerate and avoid shade, considering these as important adaptations for survival in the closed turf situations in which it frequently occurs, but did not elaborate on the mechanisms of the tolerance.

In view of the apparent contradiction concerning the shade-tolerance of yarrow (Fenner, 1978 cf., Clausen, Keck and Hiesey, 1940) and the importance of light intensity as a major environmental factor which could be manipulated by choice of crop, sowing density and time of sowing, in a programme to control yarrow on arable land, the experiment described in this section was carried out. Its aim was to determine, by the methods of growth analysis, the degree of shade tolerance, if any, displayed by the plant, and to define the mechanisms involved.

3.2 MATERIALS AND METHODS

3.2.1 Experimental procedure

The experiment was conducted in containers on a field site at Lincoln College during January and February 1979. Seed collected in March 1978, from a population on the College farm was set to germinate in moist vermiculite on 17 November 1978. Nine days later, on 26 November 1978, 500 cotyledonary seedlings were pricked out and transplanted into 500 10.0 cm polythene tubes measuring 2.0 cm in diameter and containing Wakanui silt loam soil. These plants were placed in wooden seed flats in a controlled environment growth cabinet until 24 December 1978 by which time they had developed 7 to 8 true leaves and a vigorous root

system. Sixteen hours of light per day was supplied by 48, 80 watt cool white fluorescent lamps (TL 33) and 18, 60 watt incandescent strip lights, giving 300 micro einsteins m^{-2} sec^{-1} (approximately 20% of full summer daylight). The air temperature was maintained at 23^{o} C. On 24 December 1978, one seedling was transplanted into each of 288 4.7 litre plastic liver pails, which had previously been filled with Wakanui silt loam soil and buried with their necks flush with the soil surface on the field site. Before the pails were filled, the soil was shreaded and sterilised with methyl bromide to kill weed seeds and rhizomes of couch (*Agroypron repens*) and of yarrow. Five 6 mm holes were provided in the base of each pail to allow good drainage.

The shade treatments were provided for by constructing shade houses which were erected over groups of plants in the field. Eighteen identical frames measuring 1.6 x 1.8 x 1.0 m in height were manufactured from 13 mm steel rod, to give 6 replicates of 3 shading levels. The 3 levels of shade were obtained with 3 different densities of Sarlon poly-shade cloth manufactured by Sarlon Reid Ltd, Auckland. This material was fixed on to the ends of the frames and draped from the bottom of one side, across the top and down to the base of the other side, and fastened in place with twine. The shade houses were entered to retrieve samples by releasing the cloth from the base of one side.

The cloths were rated by the manufacturers as 50%, 80% and 92% shade. These nominated transmission values were checked when the houses were in position between 1200 and 1300 hours on 19 January 1979 during which time a clear blue sky with a faint haze persisted. Replicated recordings were made at ground level inside and outside of the shade houses with a Li-cor C-275 Quantum Sensor. The amounts of photosynthetically active radiation (PAR) transmitted by the three cloths were estimated to be 46.8, 23.7 and 6.4% of full daylight; corresponding closely with the manufacturers claims for the material. The three shade fabrics were kindly tested by Mr I.J. Warrington of Plant Physiology Division, D.S.I.R., Palmerston North, to determine the spectral composition of the transmitted radiation. All three fabrics were found to be spectrally neutral (Appendix XVIII).

Groups of liver pails (Fig. 3.1) were arranged in a randomised

block design with 6 replicates. Each replicate consisted of 4 groups (treatment units) of 12 plants, in pails arranged in 3 rows of 4, with 19 cm between adjacent pails. This spacing prevented mutual shading for the duration of the experiment. The four levels of the shading treatment (100, 46.8, 23.7 and 6.4% of full daylight) were randomly allocated to each of the 6 replicates. The appropriate shade houses were then erected above the treatment units (Fig. 3.2) on 5 January 1979, 12 days after the seedlings were planted out into the pails.

The treatment units were spaced to provide a 3.0 m space between adjacent shade houses to prevent mutual shading of houses. Although there appeared to be substantial air movement through all 3 fabrics, this was assisted by providing a 5.0 cm gap between the soil surface and the base of the shade houses. Ambient air temperatures were measured both in the open and under the houses of one replicate. Recordings were taken from maximum-minimum thermometers, morning, midday and evening on three consecutive days during the experimental period (Appendix XXIII). The thermometers were mounted 5 cm above the soil on vertical cardboard shields, facing away from the sun.

The initial harvest was carried out on 5 January (at the time of imposing shade treatment), using 24 extra plants which were not included in the treatment units (Fig. 3.1). Six further harvests were taken on 12, 18, 22, 26, 30 January and 3 February 1979. On each harvest occasion, 2 plants were taken from each treatment unit on the basis of a predetermined randomisation pattern and were bulked to provide the samples from which the values of the measured parameters were obtained. The harvested plants were washed free of soil and separated into roots, rhizomes, aerial stems and leaves. The leaf area of each sample was measured with a Li-cor area meter after which all fractions were dried to a constant weight in a forced - air oven set at 85^{o} C. The dry weights of the components were subsequently ascertained and recorded.

The experiment was provided with trickle irrigation; one whisker capable of delivering 850 ml of water $pail^{-1}$ $hour^{-1}$ was supplied to each plant (Fig. 3.1). The plants were irrigated as necessary on occasions throughout the experimental period to prevent water becoming a limiting factor for growth. Weeds germinating between the pails within the treat-

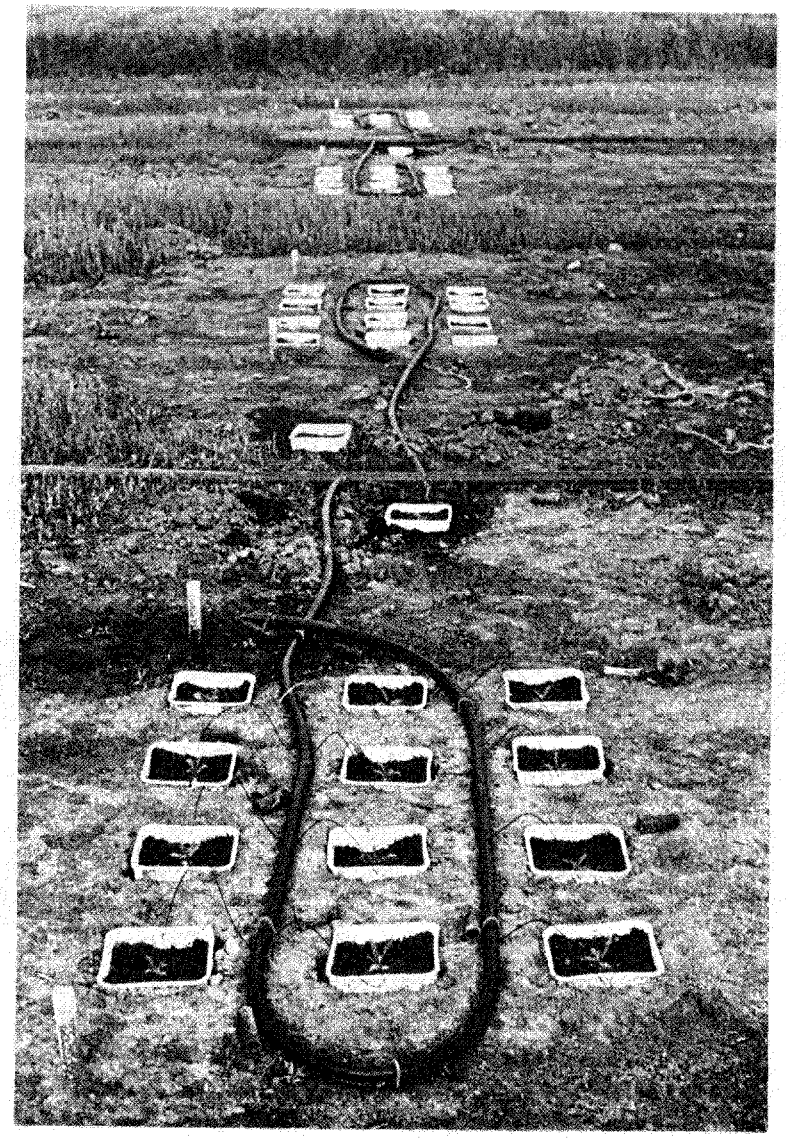


Figure 3.1 A view along one replicate before shade houses were erected, showing the layout of containers and the trickle irrigation system. Note also the plants outside the treatment units which provided initial values for measured parameters.

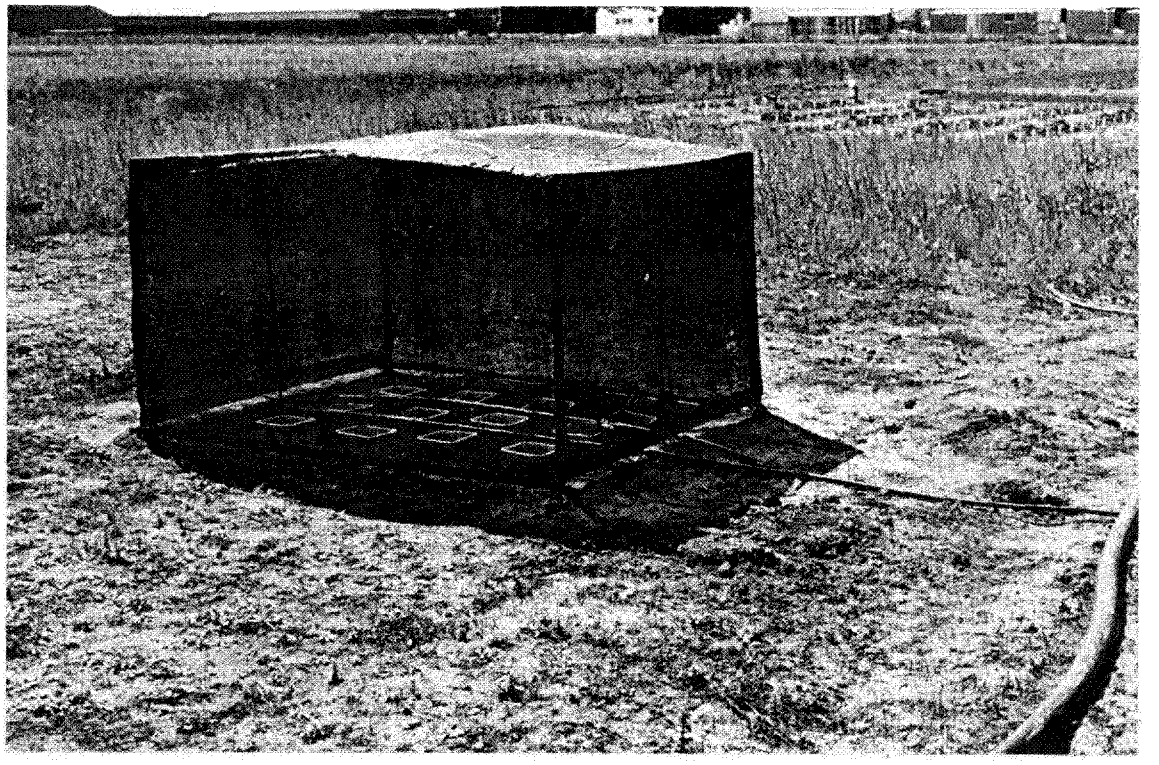


Figure 3.2 An individual shade house (46.8% full daylight) in position over a treatment unit. Note the irrigation main and lateral.

ment units were removed by hand on several occasions to prevent competition between them and the yarrow seedlings.

4.2.2 Analytical procedure

Growth analysis, using a regression technique (Appendices I and II) was performed on the data. This procedure allowed continuous time trends of the relative growth rate of total dry weight (RGR_W), leaf dry weight (RGR_{LW}), root dry weight (RGR_{RT}), stem dry weight (RGR_S), leaf area (RGR_A) and leaf area ratio (LAR), leaf weight ratio (LWR), specific leaf area (SLA) and net assimilation rate (NAR) to be estimated.

Linear regressions were used to describe the relationships between NAR, LAR and the logarithm of the relative light intensity measured in units of PAR, i.e. log PAR expressed as a percentage of full daylight. Instantaneous values of the NAR and LAR derived from the original growth analysis regression equations were used to establish these relationships. Because RGR_W = NAR x LAR, the relationship between log relative light intensity and RGR_W was derived by simply multiplying together the NAR and LAR values predicted by the linear regressions following the procedure of Blackman and Wilson (1951 b).

3.3 RESULTS

3.3.1 Time trends of growth components

The changes with time in leaf area (A), leaf dry weight (LW), total dry weight (W), root dry weight (RT) and stem dry weight (S) $plant^{-1}$ were described by polynomial regression equations, fitted to the natural logarithms of the data as specified in Appendices I and II. They represent the growth of seedling rosettes from about the 10 true leaf stage, when basal second order axes were just beginning to form (Fig. 3.15 a) until the early stages of flower stem elongation (Fig. 3.15 b) in the more advanced plants at 100% full daylight. Only a small number of short rhizomes were formed by these plants, therefore this component was not analysed except as a component of total dry weight. From these curves, the time-trends of RGR, LAR, SLA, LWR and NAR were derived as shown in Appendices I and II. The initial harvest taken at the time of imposing the treatments was not included in the curve-fitting calculations. The first harvest included

in the analysis is referred to as the first harvest. All curves are presented with confidence limits (95% probability) at each time of harvest, and the interpretation of these is also given in Appendix II. The observed means of the logarithms of A, LW, W, RT and S to which growth curves were fitted are given in Appendix III.

3.3.1.1 Leaf area The change with time in $\log_e$ leaf area was adequately explained by a linear model and it is evident in Figure 3.3 that the data fit the model extremely well. The linear regression equations for each of the four light levels are given in Table 3.1.

Table 3.1 Regression equations for $\log_e$ leaf area (A). t in days; A in cm^2

Intensity of P.A.R. as a percentage of full daylight.					
100	logA	=	4.3970	+	0.0741276t
46.8	logA	=	4.5371	+	0.0763795t
23.7	logA	=	4.4511	+	0.0779365t
6.4	logA	=	4.3699	+	0.0509702t

There are three points of interest in these relationships of $\log_e A$ to time. Firstly it can be seen that shading levels of 46.8 and 23.7% full daylight caused an increase in the total leaf area $plant^{-1}$ and that this increase was consistently maintained throughout the studied growth period. However, when shading was increased to 6.4% full daylight there was a marked and significant decline in total area. Throughout the period of measurement, the leaf areas $plant^{-1}$ were in the sequence 46.8 > 23.7 > 100 > 6.4% full daylight. The second point of interest was that the slopes of the lines for all light levels except 6.4% were very similar (Table 3.1, Fig. 3.3) indicating that the RGR_As were nearly the same. Differentiation of the equations in Table 3.1 showed the RGR_A was slightly increased with an increase in shading to 23.7% full daylight (Fig. 3.4). However, the slope of the $\log_e A$ at 6.4% was lower than at the higher light levels (Table 3.1) and differentiation revealed a significantly

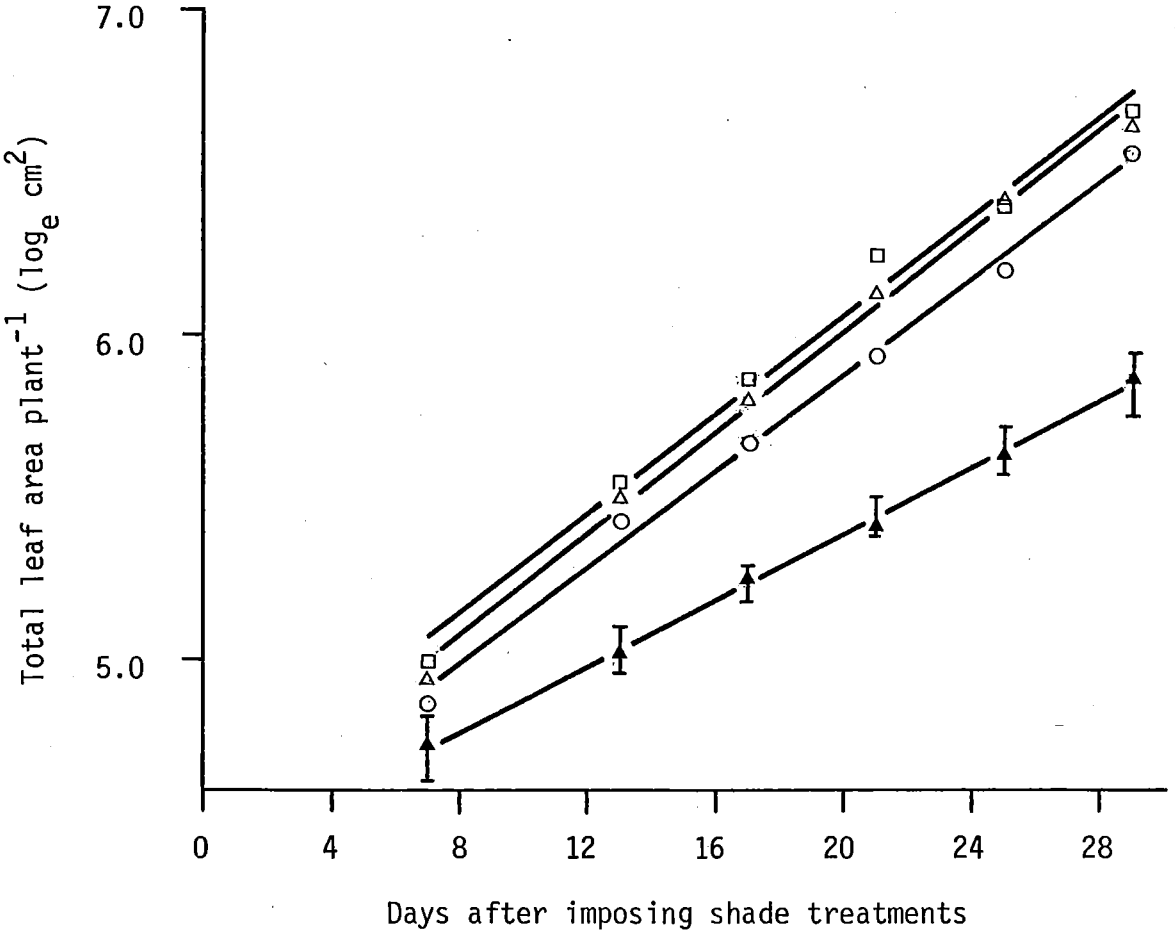


Figure 3.3 Progress curves of leaf area plant^{-1}. The points are the observed means of the logarithms for the six replicates, each of two plants. The lines are the linear curves fitted to all individual samples (replicates) and the bars are the confidence limits for the fitted values (95% probability).

○ —— ○, 100% of full daylight; □ —— □, 46.8% of full daylight; △ —— △, 23.7% of full daylight; ▲ —— ▲, 6.4% of full daylight.

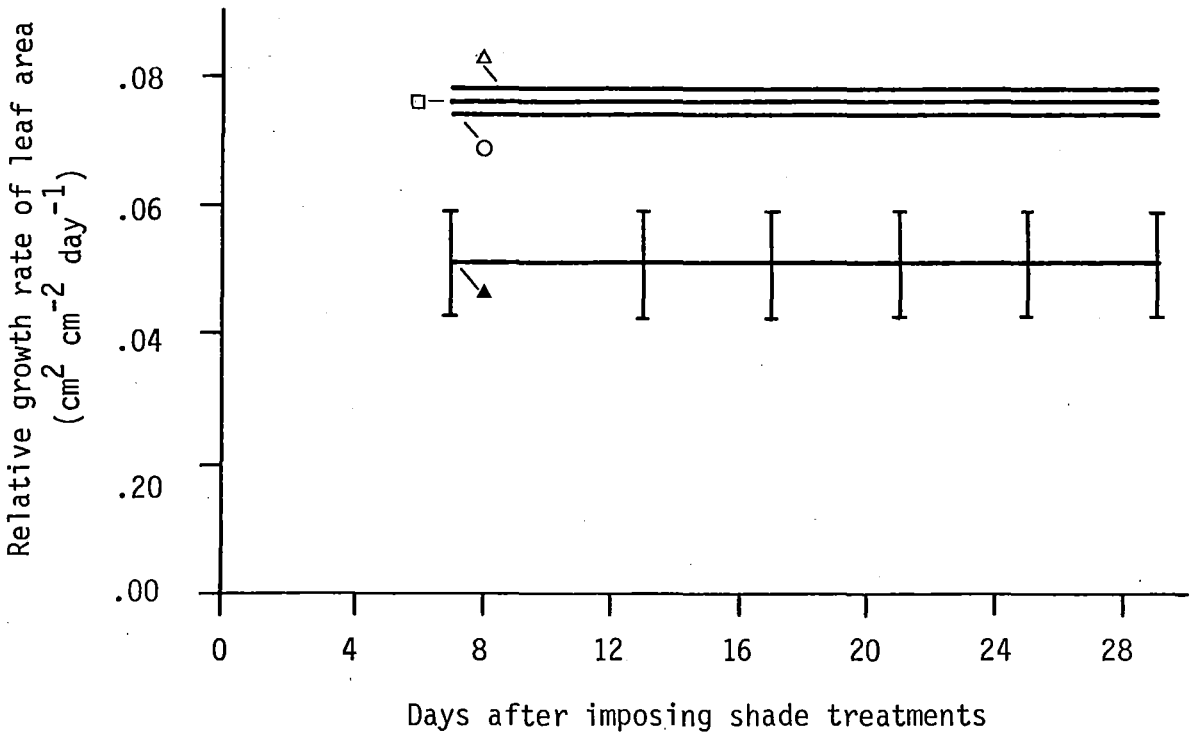


Figure 3.4 Progress curves of relative growth rate of leaf area, derived by differentiation from Figure 3.3. Lines from fitted linear equations; bars are the confidence limits for means of six replicate samples (95% probability).

○, 100% of full daylight; □, 46.8% of full daylight; △, 23.7% of full daylight; ▲, 6.4% of full daylight.

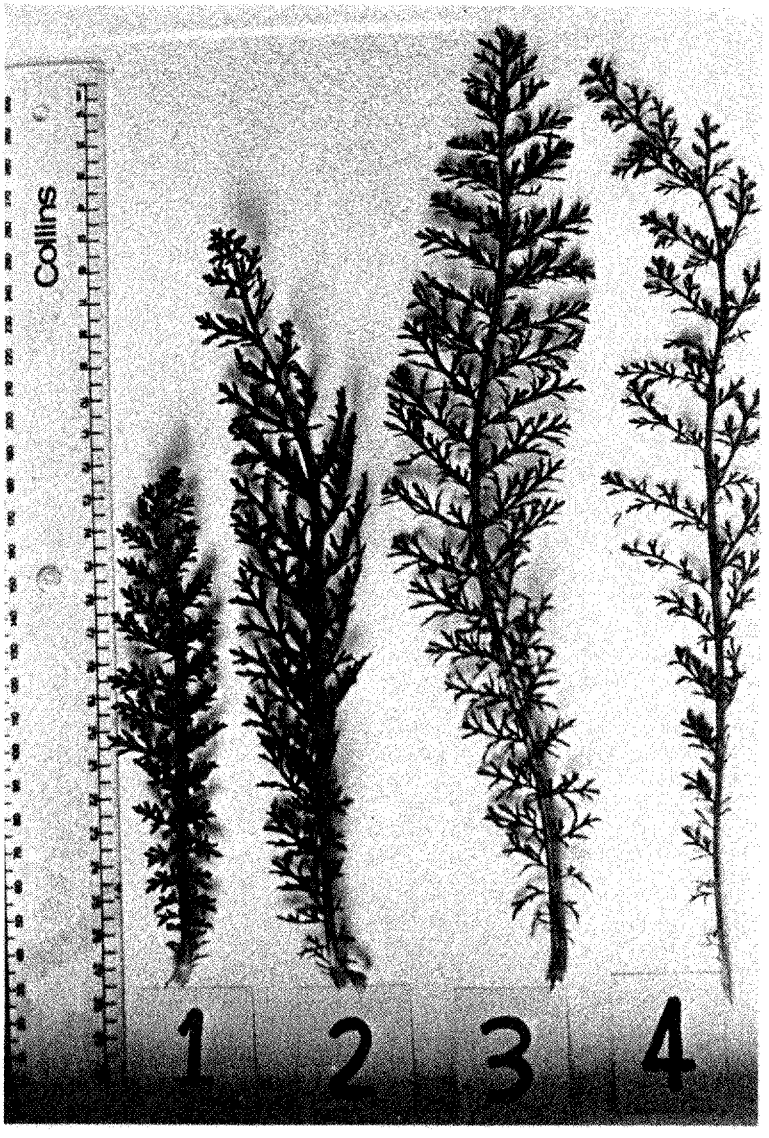


Figure 3.5 Fully expanded rosette leaves showing typical responses to reduction in the intensity of photosynthetically active radiation. 1. 100% of full daylight; 2. 46.8% of full daylight; 3. 23.7% of full daylight; 4. 6.4% of full daylight. The photograph was taken 29 days after imposing the shade treatments (3 February 1979); cf., Figure 3.15 b.

lower RGR_A at this low level of light (Fig. 3.4). Thirdly, as a consequence of the linearity of the $\log_e A$ progress with time, the RGR_A was constant throughout the experimental period (Fig. 3.4). It can also be seen in Figure 3.3 that the shade treatments had affected the leaf area plant^{-1} 7 days after they were imposed.

3.3.1.2 Leaf dry weight Leaf dry weight plant^{-1} increased with time at all levels of shading but in contrast to $\log_e A$, the trend of $\log_e$ LW was best described by a quadratic model (Fig. 3.6). In spite of the increased leaf area plant^{-1} at shading levels of 46.8 and 23.7% full daylight, leaf dry weights declined with increased shading and lay in the order 100 > 46.8 > 23.7 > 6.4% full daylight. The reduction from the value in full daylight was only slight at 46.8%, greater at 23.7% and substantial at 6.4% full daylight (Fig. 3.6). The slopes (t coefficient) and negative curvatures (t^2 coefficients) of $\log_e LW$ at 100% and 46.8% were much the same (Table 3.2) indicating a similar magnitude and rate of decline of RGR_{LW} for these two light levels (Fig. 3.7). At 23.7% full daylight t^2 was still negative, but smaller than for 46.8 and 100%, differentiation showing the RGR_{LW} at this light level declined less rapidly with time (Fig. 3.7). In sharp contrast to light intensities of 100, 46.8 and 23.7% full daylight, at 6.4%, the t^2 coefficient was small, but positive, and therefore the RGR_{LW} at this low light level tended to rise with time. As was the case with the changes brought about in leaf area, the reductions in leaf dry weight were apparent by the time of the first harvest, taken 7 days after imposition of the shade treatments (Fig. 3.6).

Table 3.2 Regression equations for $\log_e$ leaf dry weight (LW). t in days; LW in g.

Intensity of P.A.R. as a percentage of full daylight						
100	logLW	=	-1.0434	+	0.1378581t	$-0.001457943t^2$
46.8	logLW	=	-1.1914	+	0.1405628t	$-0.001493045t^2$
23.7	logLW	=	-1.2209	+	0.1121074t	$-0.000796641t^2$
6.4	logLW	=	-1.1474	+	0.0449183t	$+0.000179806t^2$

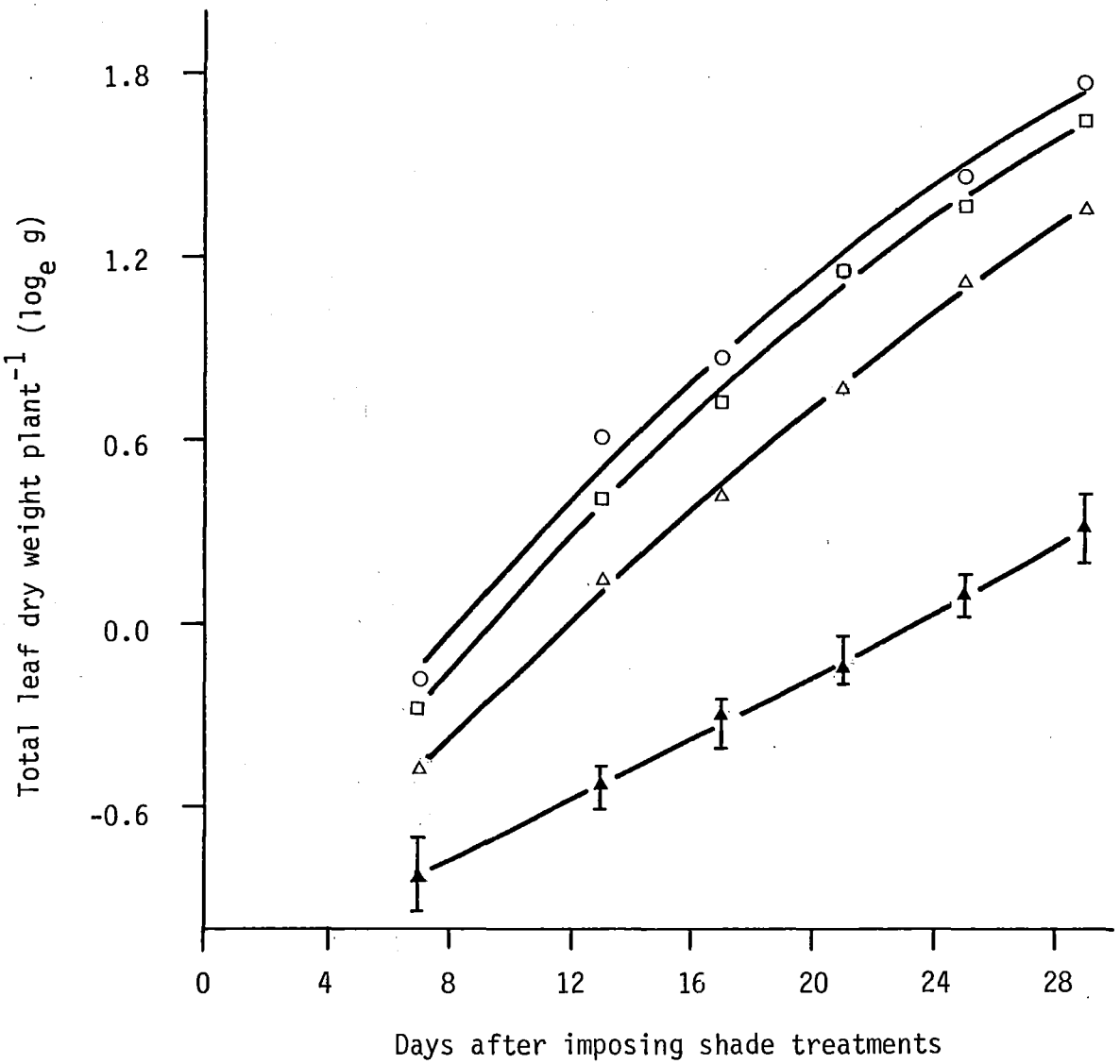


Figure 3.6 Progress curves of leaf dry weight plant^{-1}. The points are the observed means of the logarithms for six replicates, each of two plants. The lines are the quadratic curves fitted to all individual samples (replicates) and the bars are the confidence limits for the fitted values (95% probability). Symbols as in Figure 3.3.

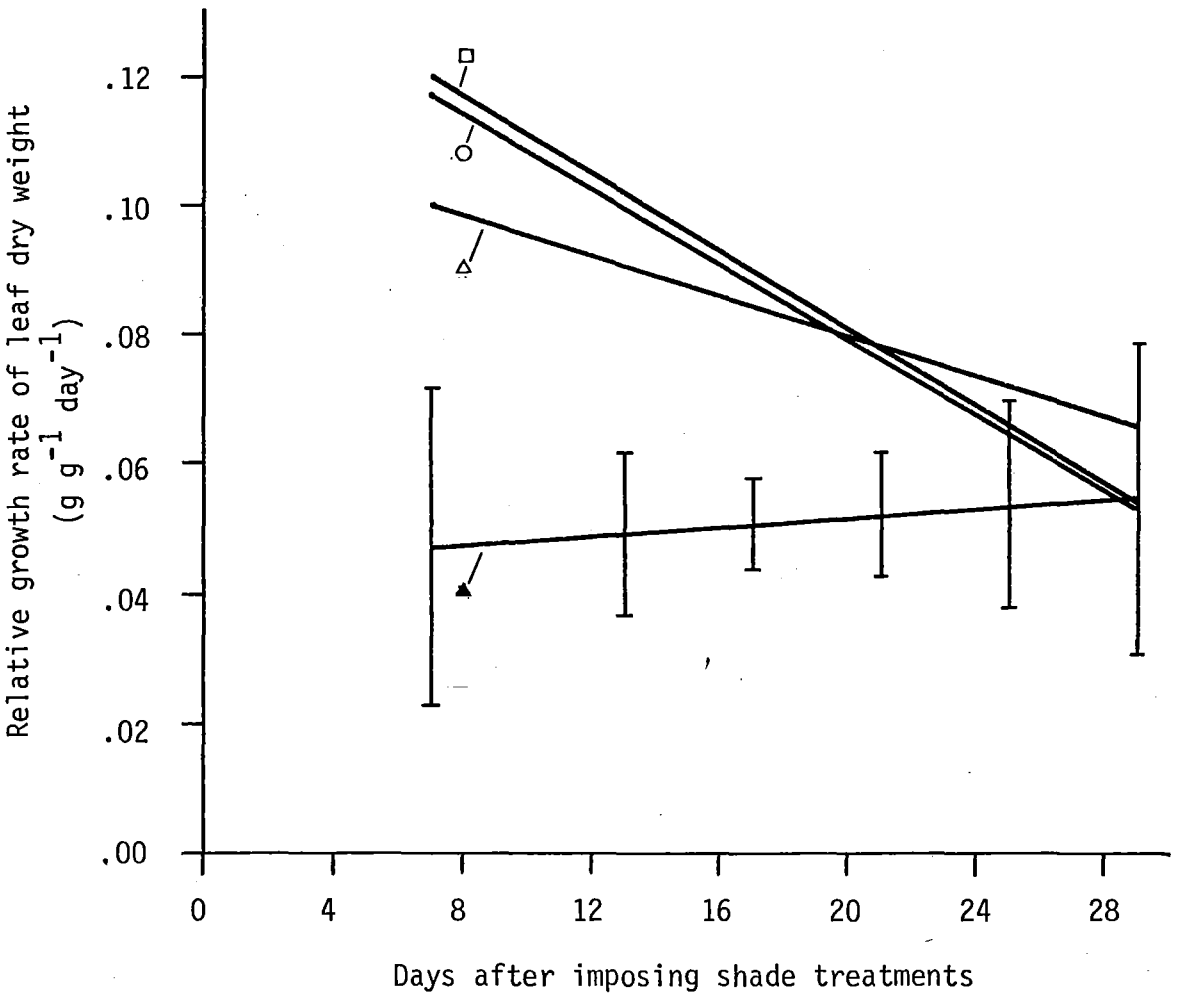


Figure 3.7 Progress curves of relative growth rate of leaf dry weight, derived by differentiation from Figure 3.6. Lines from fitted quadratics; bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4.

3.3.1.3 Total dry weight Total dry weight plant^{-1} increased with time at all light levels, and the change in the logarithms was described by a quadratic model (Fig. 3.8). It is evident that the responses of $\log_e W$ with time and shading were very similar to the responses of $\log_e$ LW (compare Figs. 3.8 and 3.6 and Tables 3.3 and 3.2). As a result of these similarities of $\log_e W$ with $\log_e LW$, the RGR_W at 100, 46.8 and 23.7% full daylight was of similar magnitude and declined at a similar rate with time (compare Figs. 3.10 and 3.7). As with RGR_{LW}, throughout the experimental period the RGR_W at 46.8% full daylight was unchanged from the value in full daylight. However, at 6.4% full daylight, the t coefficient for $\log_e W$ was lower than for $\log_e LW$ and the t^2 coefficient was higher (Tables 3.3 and 3.2) resulting in RGR_W being generally lower than RGR_{LW} but increasing more rapidly with time (Figs. 3.10 and 3.7). It was clear that dry weight plant^{-1} was reduced by shading at all levels and that this response was manifest by the time of the first harvest, after 7 days of shade treatment (Fig. 3.8).

Table 3.3 Regression equations for $\log_e$ total dry weight (W). t in days; W in g.

Intensity of P.A.R. as a percentage of full daylight.						
100	logW	=	-0.50665	+	0.1433094t	$-0.001523805t^2$
46.8	logW	=	-0.72906	+	0.1447078t	$-0.001545272t^2$
23.7	logW	=	-0.75605	+	0.1052200t	$-0.000546879t^2$
6.4	logW	=	-0.58383	+	0.0235667t	$+0.000579917t^2$

In order to illustrate clearly the true magnitude of the effect of the shading levels on total dry matter accumulation by the seedlings, the fitted $\log_e W$ lines (Fig. 3.8) were backtransformed and are presented in Figure 3.9. The backtransformed means of the logarithms of the measured dry weights (Appendix III) presented as points about the lines, demonstrate the closeness of fit of the data to the quadratic model for $\log_e W$.

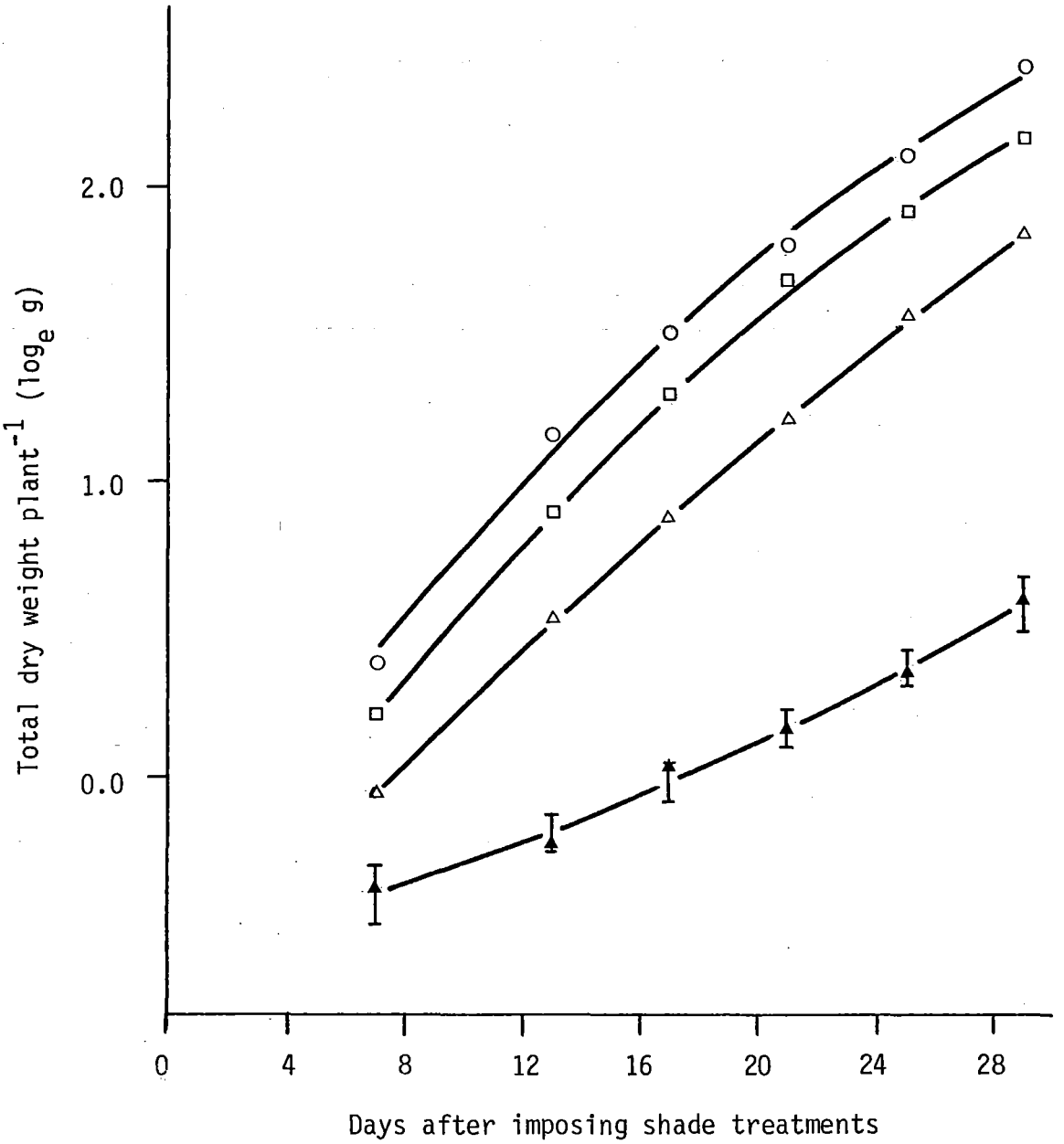


Figure 3.8 Progress curves of total dry weight plant^{-1}. The points are the observed means of the logarithms for six replicates, each of two plants. The lines are the quadratic curves fitted to all individual samples (replicates) and the bars are the confidence limits for the fitted values (95% probability). Symbols as in Figure 3.3

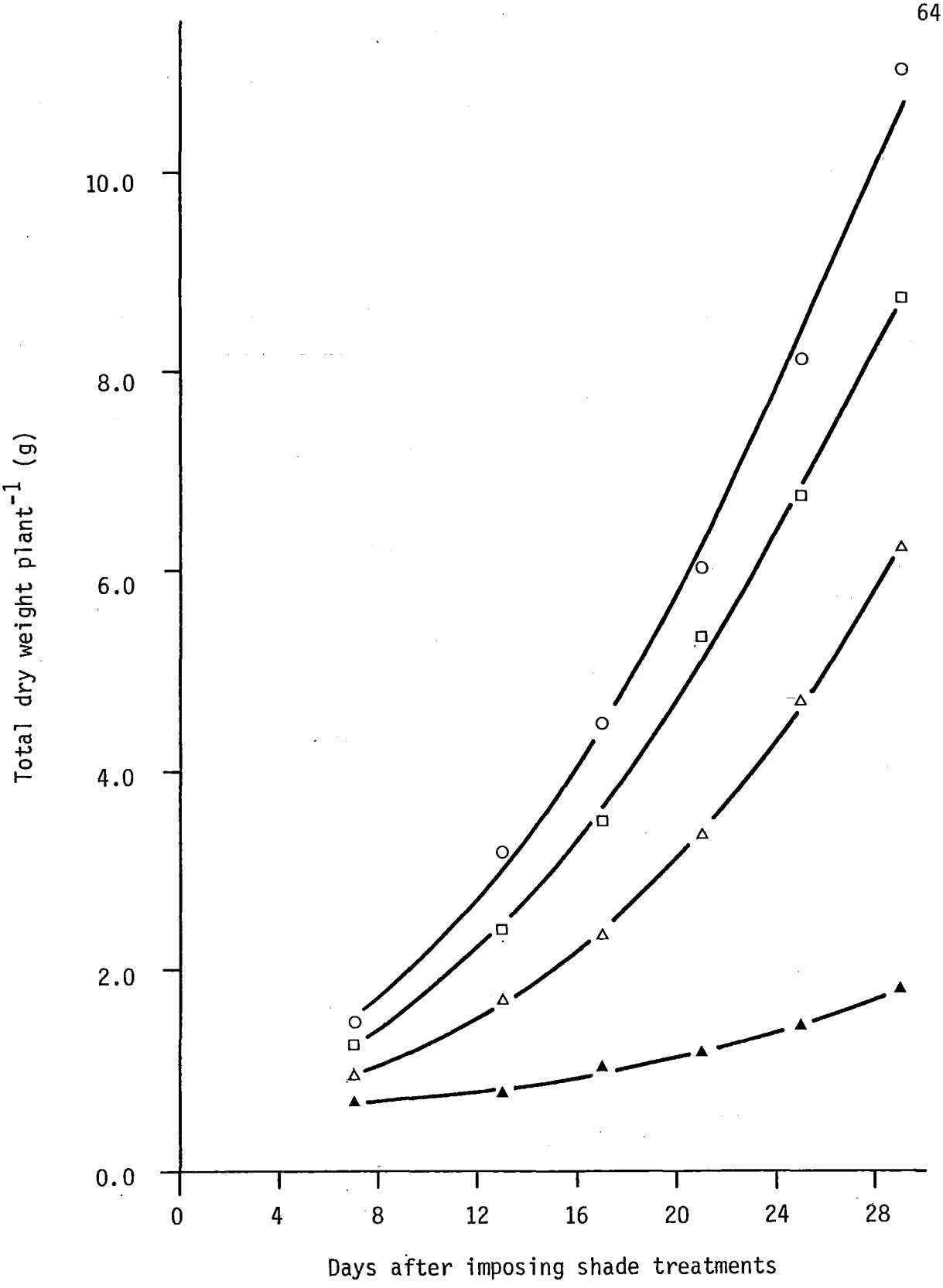


Figure 3.9 Progress curves of total dry weight plant^{-1}. The points are the back-transformed observed means of the logarithms from Figure 3.8 and the lines are the back-transformed fitted values from Figure 3.8. Symbols as in Figure 3.3.

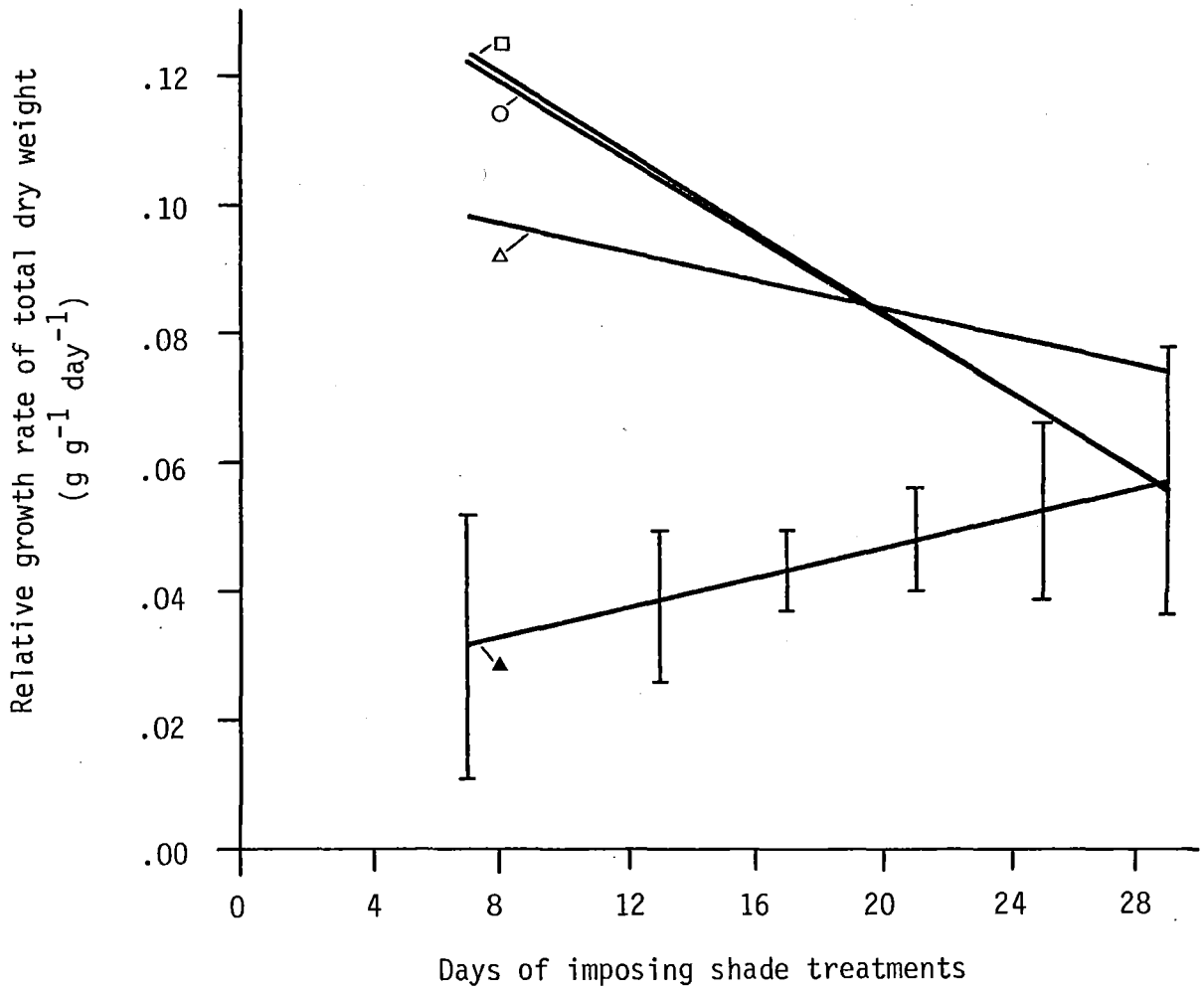


Figure 3.10 Progress curves of relative growth rate, derived by differentiation from Figure 3.8. Lines from fitted quadratics; bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4.

3.3.1.4. Root dry weight A quartic regression model was found necessary to adequately describe the changes in the logarithms of root dry weight plant^{-1} with time (Fig. 3.11). The equations of the fitted curves are given in Table 3.4. It is evident that such a complex growth function as this was necessary as a consequence of the complicated relationship of $\log_e$RT to time at the lowest light level (6.4% full daylight). At all light levels except 6.4% full daylight, root dry weight increased with time, but was substantially reduced as the shading level was increased (Fig. 3.11), this reduction being evident from the time of the first harvest, 7 days after shading began. At these light levels the general slope of the $\log_e$RT curves were similar and upon differentiation of the equations given in Table 3.4 the RGR_{RT}s were revealed to be of the same magnitude and to generally decline with time (Fig. 3.12).

Table 3.4 Regression equations for $\log_e$ root dry weight (RT) .t in days; RT in g.

Intensity of P.A.R. as a percentage of full daylight.						
100	logRT	=	-2.5957	+0.4528355t	-0.030813795t^2	+0.001121473t^3 -0.000015296t^4
46.8	logRT	=	-1.2868	+0.0056925t	+0.008825256t^2	-0.000317467t^3 +0.000003318t^4
23.7	logRT	=	-0.6891	-0.2653377t	+0.033650369t^2	-0.001322984t^3 +0.000018005t^4
6.4	logRT	=	4.5545	-1.7308622t	+0.161807010t^2	-0.006163284t^3 +0.000082936t^4

The inflections at the extremities of the curves for RGR_{RT} at 100 and 23.7% full daylight are a function of the complexity of the equations describing $\log_e$RT and cannot be considered as biologically sound. The large size of the confidence limits (95% probability) at the ends of these curves show how little confidence can be placed in the fitted values of $\log_e$RT in these regions of the curves. At 6.4% full daylight root dry

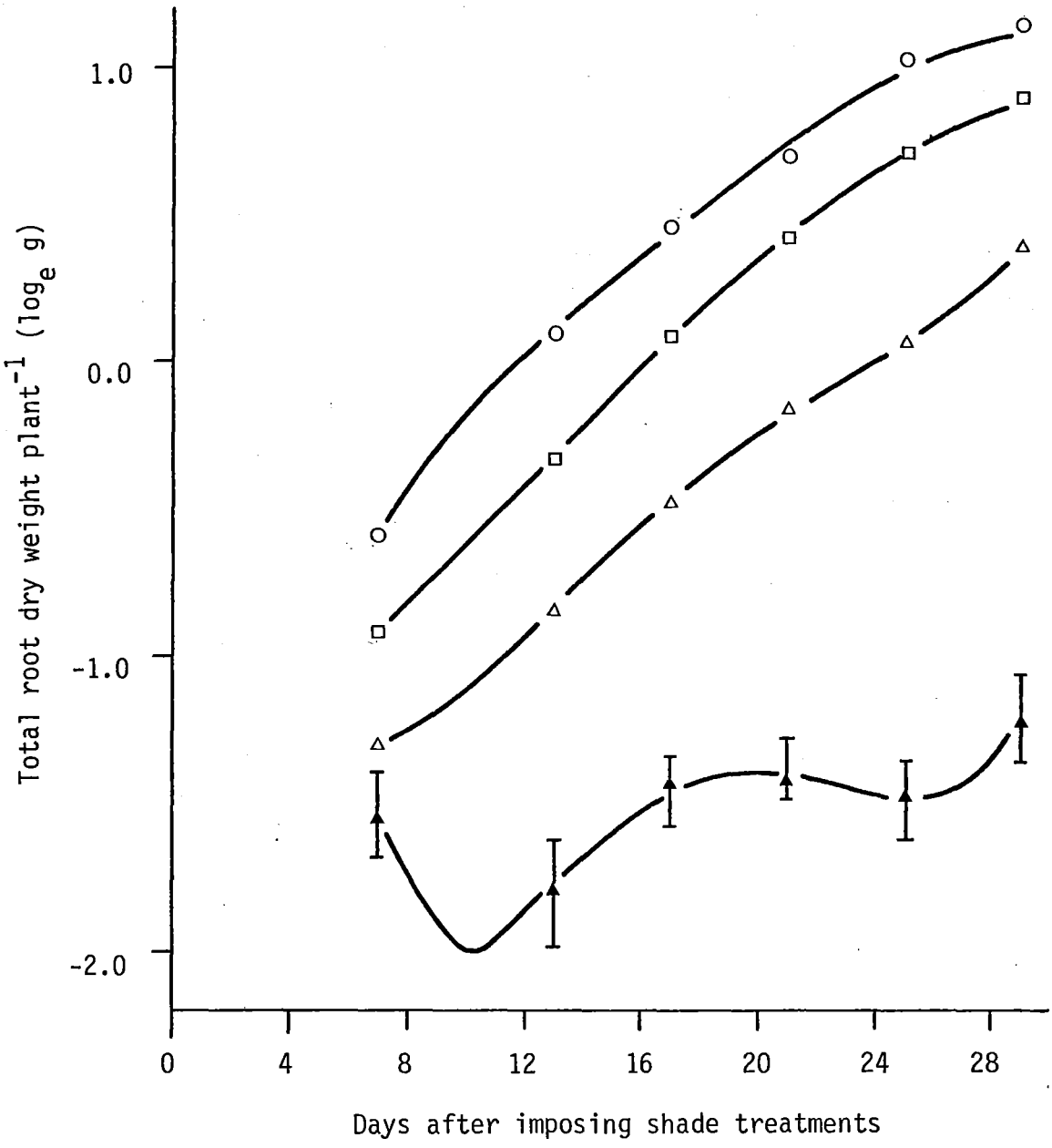


Figure 3.11 Progress curves of root dry weight plant^{-1}. The points are the observed means of the logarithms for six replicates, each of two plants. The lines are the quartic curves fitted to all individual samples (replicates) and the bars are the confidence limits for the fitted values (95% probability). Symbols as in Figure 3.3.

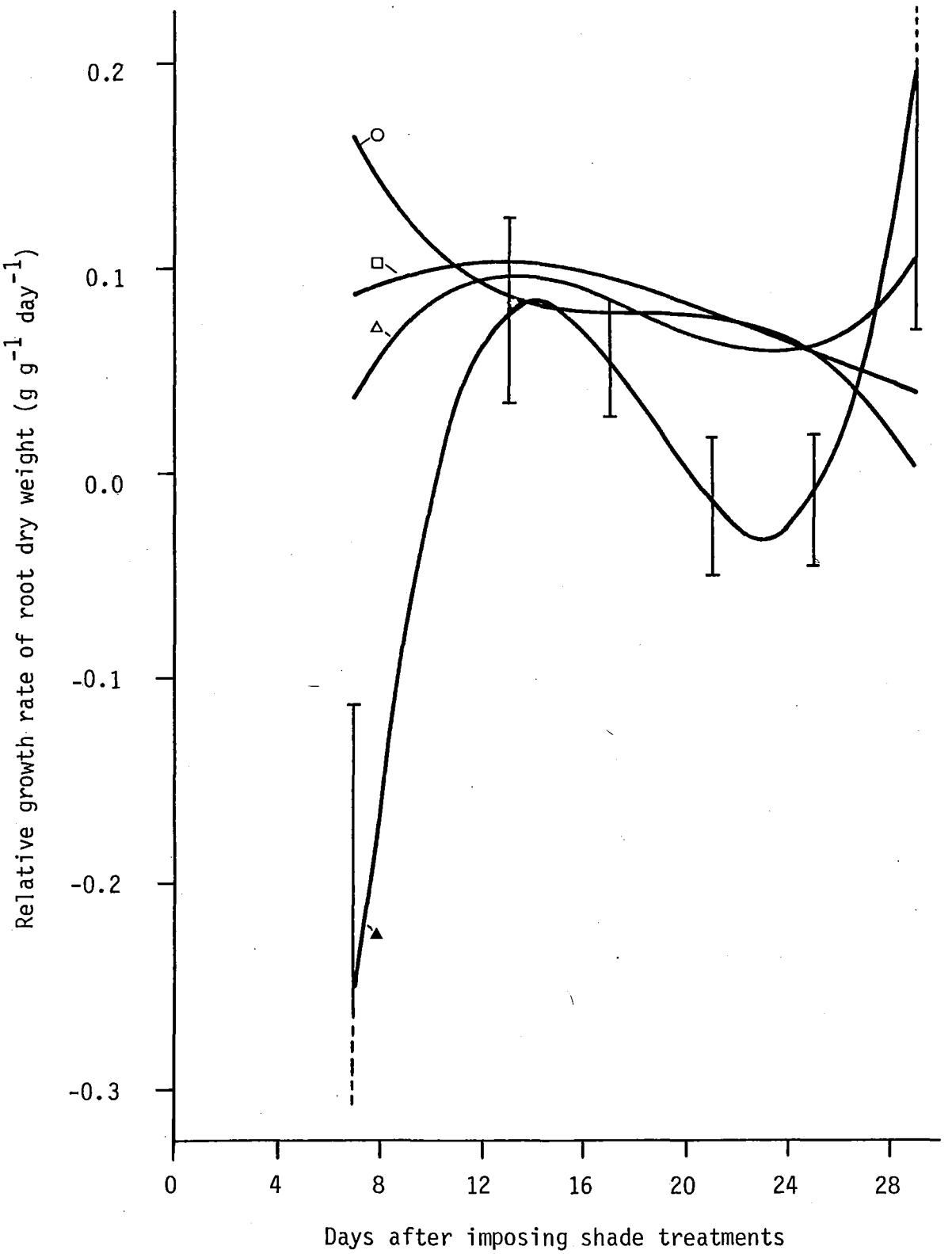


Figure 3.12 Progress curves of relative growth rate of root dry weight, derived from Figure 3.11 by differentiation. Lines from fitted quartics; bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4.

weight plant^{-1} was markedly depressed in comparison with the other light levels (Fig. 3.11), and in contrast showed an initial decline with time. Root dry weight did not increase above the value at day 7 until some 9 or 10 days later at day 16-17. The rise in root weight then continued until day 21 when a further decline followed by a subsequent rise occurred. These losses and gains of root dry matter at 6.4% full daylight are reflected in the widely oscillating RGR_{RT} (Fig. 3.12). During the period of positive root growth and recovery from the initial loss in weight, dry matter accumulation in the root system at 6.4% full daylight reached a peak in efficiency (day 14) similar to the maximum at the other light intensities (Fig. 3.12). However this was soon followed by a rapid decline in RGR_{RT}, and by day 20 it was negative, the root system apparently again losing weight.

3.3.1.5 Stem dry weight and elongation Stem dry weight plant^{-1} increased with time in a complicated manner at all light intensities (Fig. 3.13). Because of this complexity, it was necessary to fit quartic regressions to $\log_e S$ to provide an adequate description of the changes in dry weight with time (Table 3.5). Shading to 46.8% full daylight had little effect on the amount of stem dry matter plant^{-1} but at 23.7% there was a significant reduction whilst at 6.4% full daylight a very marked decrease occurred. At all light intensities, the $\log_e S$ curves were characteristed by an initial phase of slight increase preceding a phase of more rapid increase, only to be followed by a lower rate of increase and then an abrupt rise. This pattern of increase in stem dry weight is more readily apparent after deriving the RGR_Ss (Fig. 3.14). It can be seen that the RGR_Ss were similar in magnitude and rate of change with time and that although stem growth was slow in the early stages of the experiment, RGR_Ss rose sharply to 0.2 g g^{-1} day^{-1} in all but 6.4% full daylight. Such high relative rates of increase were not found for any of the other plant components. The RGR_Ss then fell towards the later stages of the experimental period at which time a very sudden increase was apparent, marking the beginning of stem bolting. This is illustrated in plants representative of the four shading levels at the final harvest on 3 February (Fig. 3.15b).

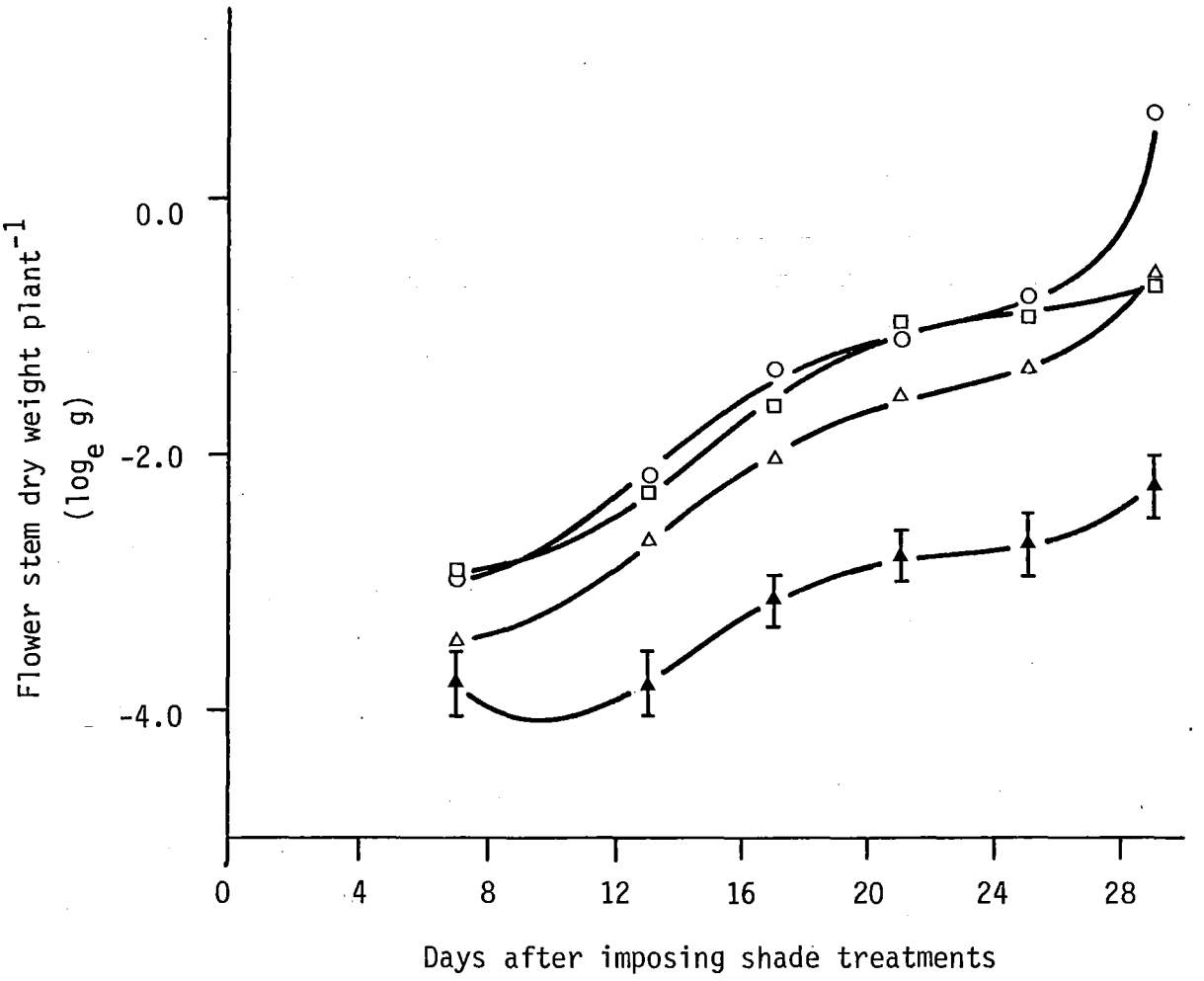


Figure 3.13 Progress curves of flower stem dry weight plant^{-1}. The points are the observed means of the logarithms for six replicates, each of two plants. The lines are the quartic curves fitted to all individual samples (replicates) and the bars are the confidence limits for the fitted values (95% probability). Symbols as in Figure 3.3.

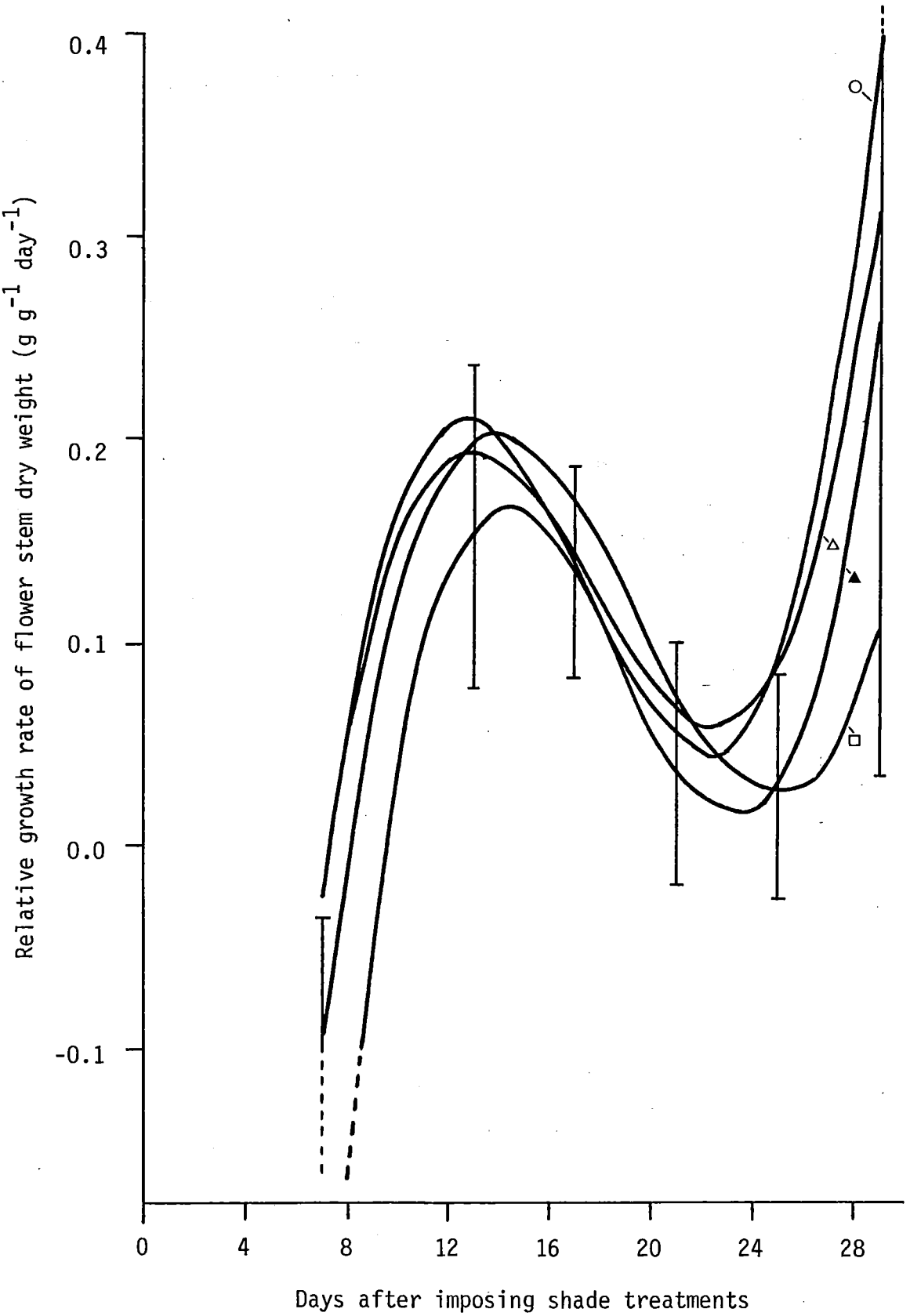
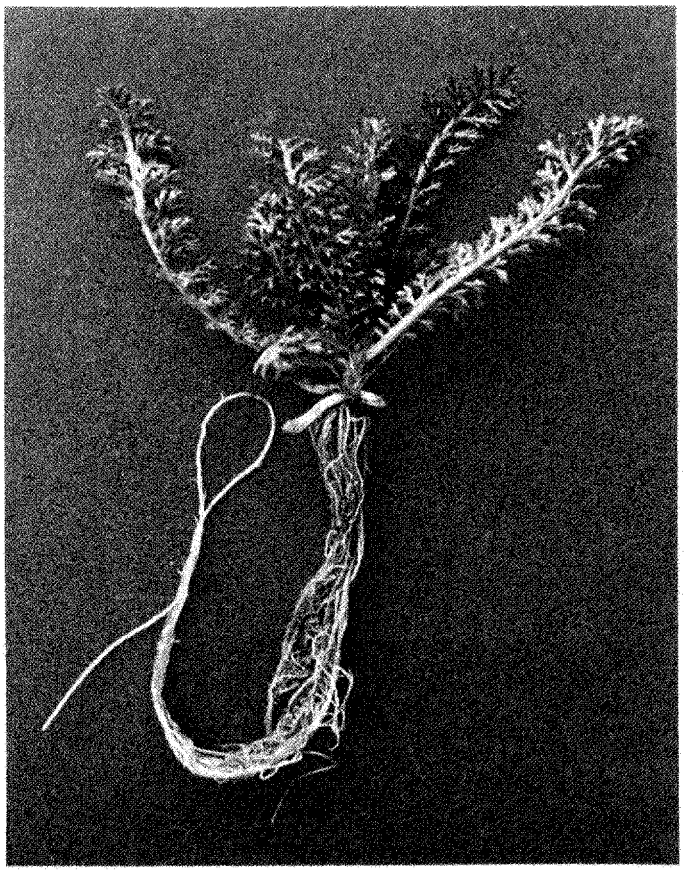


Figure 3.14 Progress curves of relative growth rate of stem dry weight, derived by differentiation from Figure 3.13. Lines from fitted quartics; bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4.

a)



b)

Figure 3.15 Experimental plants; a) a seedling at the time of initial harvest and imposition of shade treatments (5 January 1979); b) representative plants from each of the four shade levels at the time of final harvest (3 February 1979). Treatments 1, 2, 3 and 4 are respectively : 100, 46.8, 23.7 and 6.4% of full daylight.

Table 3.5 Regression equations for $\log_e$ stem dry weight (S) .t in days; S in g.

Intensity of P.A.R. as a percentage of full daylight.			
100	$\log S$ =	$1.1306 - 1.3921067t + 0.155907508t^2 - 0.006432859t^3 + 0.00009203t^4$	
46.8	$\log S$ =	$1.4239 - 1.3537733t + 0.137596611t^2 - 0.005135091t^3 + 0.00006601t^4$	
23.7	$\log S$ =	$0.07934 - 1.1961069t + 0.132637187t^2 - 0.00536854t^3 + 0.000075524t^4$	
6.4	$\log S$ =	$3.6067 - 2.1366785t + 0.20244658t^2 - 0.007604795t^3 + 0.000100843t^4$	

The effect of shading on the frequency of flower stem formation is presented in Table 3.6. Stems with elongating internodes were first apparent at all shading levels at the time of the third harvest, 17 days after imposing the shade treatments. It can be seen that shading to 46.8% full daylight did not affect the percentage of plants forming stems but at 23.7% and most markedly, at 6.4%, there was a reduction.

Table 3.6 The effect of shading on flower stem formation (values are the percentages of plants showing elongation of primary and/or secondary axes based on 12 plants (6 replicates of 2 plants) per treatment; actual number in parenthesis).

days after imposing shade	light intensity (% full daylight) 100	46.8	23.7	6.4
7	0	0	0	0
13	0	0	0	0
17	58 (7)	58 (7)	58 (7)	8 (1)
21	58 (7)	83 (10)	58 (7)	8 (1)
25	83 (10)	67 (8)	67 (8)	8 (1)
29	83 (10)	75 (9)	75 (9)	8 (1)
mean	71	71	65	8

3.3.1.6 Leaf area ratio, leaf weight ratio, specific leaf area

The trends of LAR with time and the effect of the four levels of shading are presented in Figure 3.16. It is immediately clear that shading has induced a considerable increase in this growth function, the values consistently lying in the sequence, 100 < 46.8 < 23.7 < 6.4% full daylight. From the time of the first harvest on day 7 (7 days after shading began), there was a steady fall in this ratio with time at shading levels of 100, 46.8 and 23.7% full daylight. This decline stopped after 22 to 25 days and there appeared to be an increase in the later part of the experimental period. In contrast to this decline in LAR, a pronounced increase with time occurred at 6.4% full daylight, and a maximum was reached at day 24 (Fig. 3.16). It is evident in Figure 3.16 that during the 7 - day period between imposing the shade treatments and the first harvest, LAR increased at 46.8, 23.7 and 6.4% full daylight, but declined during this period at 100% full daylight.

The components of LAR, i.e. SLA and LWR are presented in Figures 3.17 and 3.18 respectively. Looking first at SLA (Fig. 3.17) it can be seen that shading brought about a substantial increase in this ratio, showing that the leaves became thinner when the plants were progressively more heavily shaded. The values of SLA were consistently in the order 100 < 46.8 < 23.7 < 6.4% full daylight. With the progress of time, the SLA at 100, 46.8 and 23.7% full daylight declined (leaves became thicker) and reached a minimum by day 22 after which an increase appeared to take place. At 6.4% full daylight, the SLA remained almost constant throughout most of the experimental period, and declined slightly near the end of the period (Fig. 3.17). As was the case with LAR, SLA increased during the 7 - day period from the beginning of shading until the first harvest at 46.8, 23.7 and 6.4%, but declined at 100% full daylight.

The LWR also increased significantly as the degree of shading was increased (Fig. 3.18), and except for the similarity between the day - 7 values at 23.7 and 6.4% full daylight, they lay in the sequence 100 < 46.8 < 23.7 < 6.4% full daylight. Therefore shading caused the plants to allocate a greater proportion of their total dry matter to leaf tissue. At all shading levels except 6.4% full daylight, LWR declined gently with time from day 7 onwards, and also declined from the time of the initial

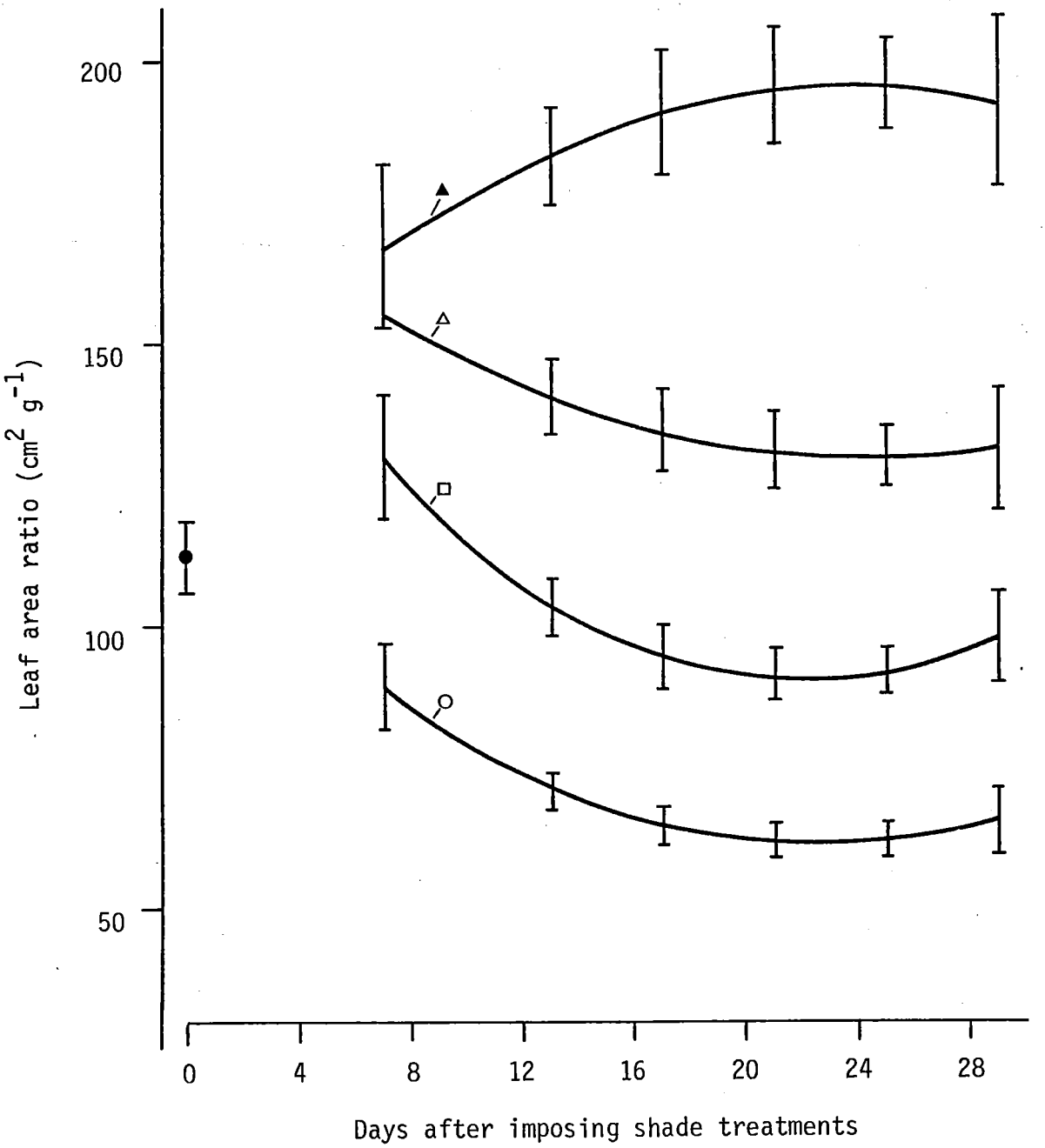


Figure 3.16 Progress curves of leaf area ratio. Lines are from the fitted $\log_e A$ (Figure 3.3) and $\log_e W$ (Figure 3.9) by subtraction; bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4. ●, initial value prior to imposing shade treatments.

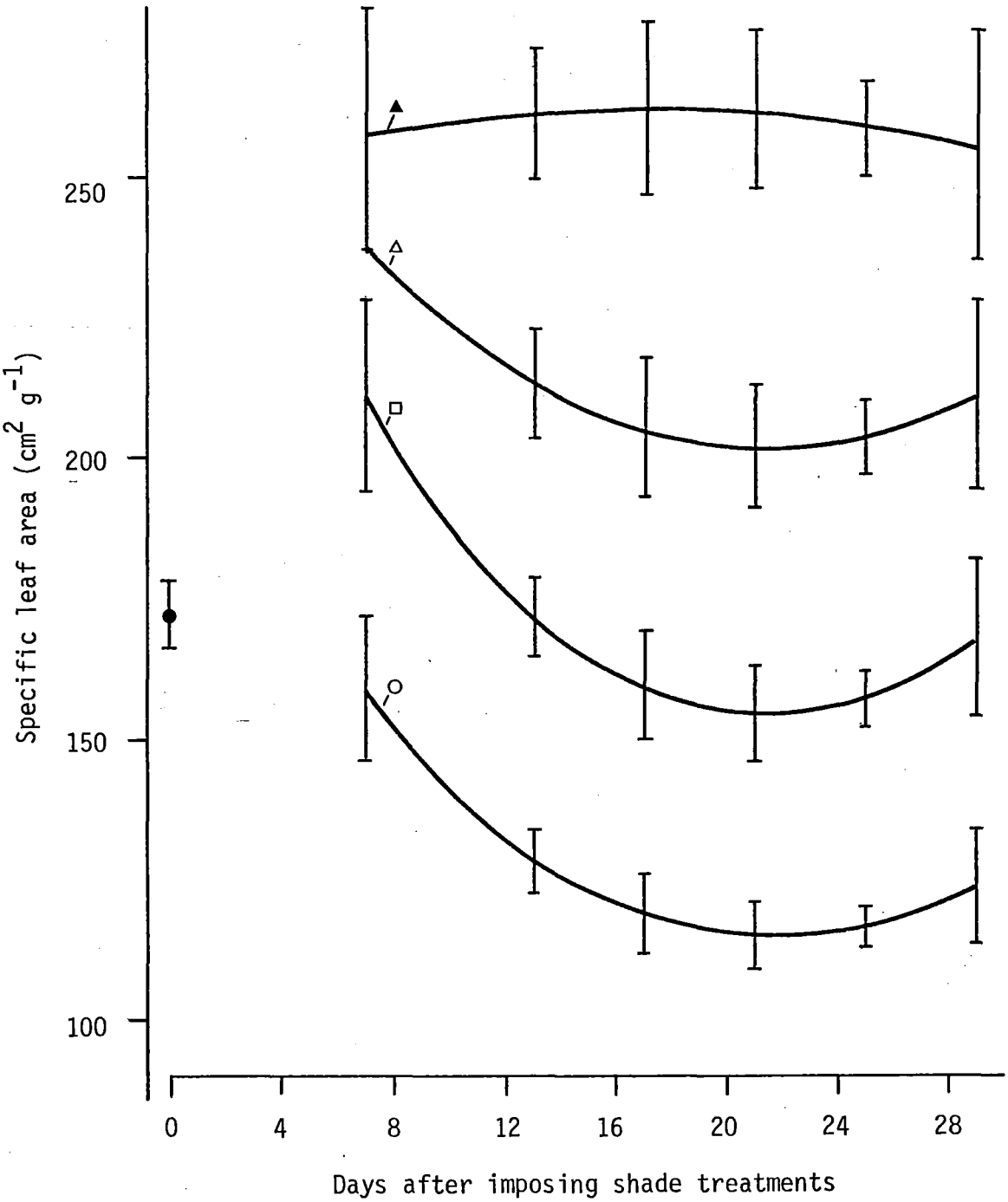


Figure 3.17 Progress curves of specific leaf area. Lines are from the fitted $\log_e A$ (Figure 3.3) and $\log_e LW$ (Figure 3.6) by subtraction; bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4 and 3.16.

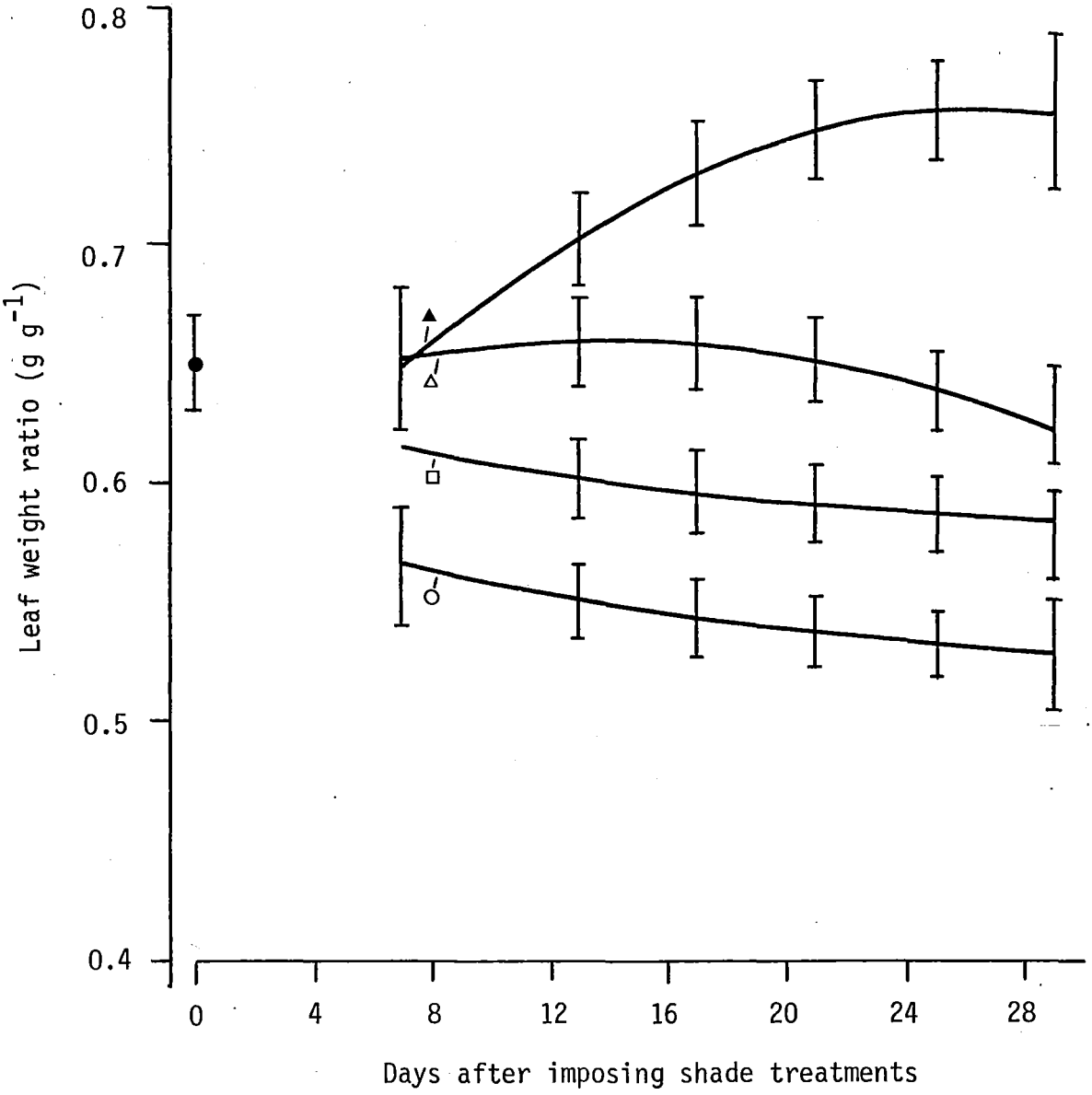


Figure 3.18 Progress curves of leaf weight ratio. Lines are from the fitted $\log_e LW$ (Figure 3.6) and $\log_e W$ (Figure 3.9) by subtraction; bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4 and 3.16.

harvest until day 7 when shading began, at 100 and 46.8%, but increased slightly during this period at 23.7% full daylight. In contrast to SLA, LWR at 6.4% full daylight increased markedly with time until by day 27 these plants had allocated 75% of their dry matter to leaf tissue, compared to 63% at 23.7% full daylight, 58.5% at 46.8% full daylight and 53% at 100% full daylight.

From this breakdown of the LAR it is apparent that the increase in this ratio with increased shading (Fig. 3.16) was brought about by both a decrease in leaf thickness (increased SLA, Fig. 3.17) and an increase in the proportion of total plant dry matter allocated to leaf tissue (increased LWR, Fig. 3.18). The downward trend with time at light levels other than 6.4% full daylight was predominantly a consequence of declining SLA (Fig. 3.17) but was also contributed to by the falling LWR (Fig. 3.18). The marked increase in LAR with time at 6.4% full daylight (Fig. 3.16) was almost entirely the result of the increase in LWR (Fig. 3.18) because the SLA remained almost constant through time (Fig. 3.17).

3.3.1.7 Net assimilation rate The response of NAR to shading and the trends with time are presented in Fig. 3.19. It can be seen that shading caused a substantial reduction in NAR, and except for the similarity between the rates for 46.8 and 23.7% full daylight at day 29, the NARs were consistently in the sequence 100 > 46.8 > 23.7 > 6.4% full daylight. This effect was evident 7 days after imposing the shade treatments but was reduced with time due to the decline in NAR during the second half of the experimental period at 100 and 46.8% full daylight, the almost constant rate at 23.7% and an increasing rate at 6.4% full daylight.

3.3.2 Trends of growth components with increasing plant dry weight

In order to discover the effect of plant size as distinct from chronological age, on the growth attributes, and hence to allow a comparison of the effects of shading on plants at comparable and constant size, the estimates of LAR, SLA, LWR, NAR and RGR which were derived from the fitted regression equations, were plotted against total dry weight plant^{-1} (Fig. 3.20). These curves show, more clearly than do the time-trends, the developmental or ontogenetic changes in the growth functions. Allowance must be made for any ontogenetic changes if the effects of environmental factors which alter the rate of physiological development are to be validly assessed.

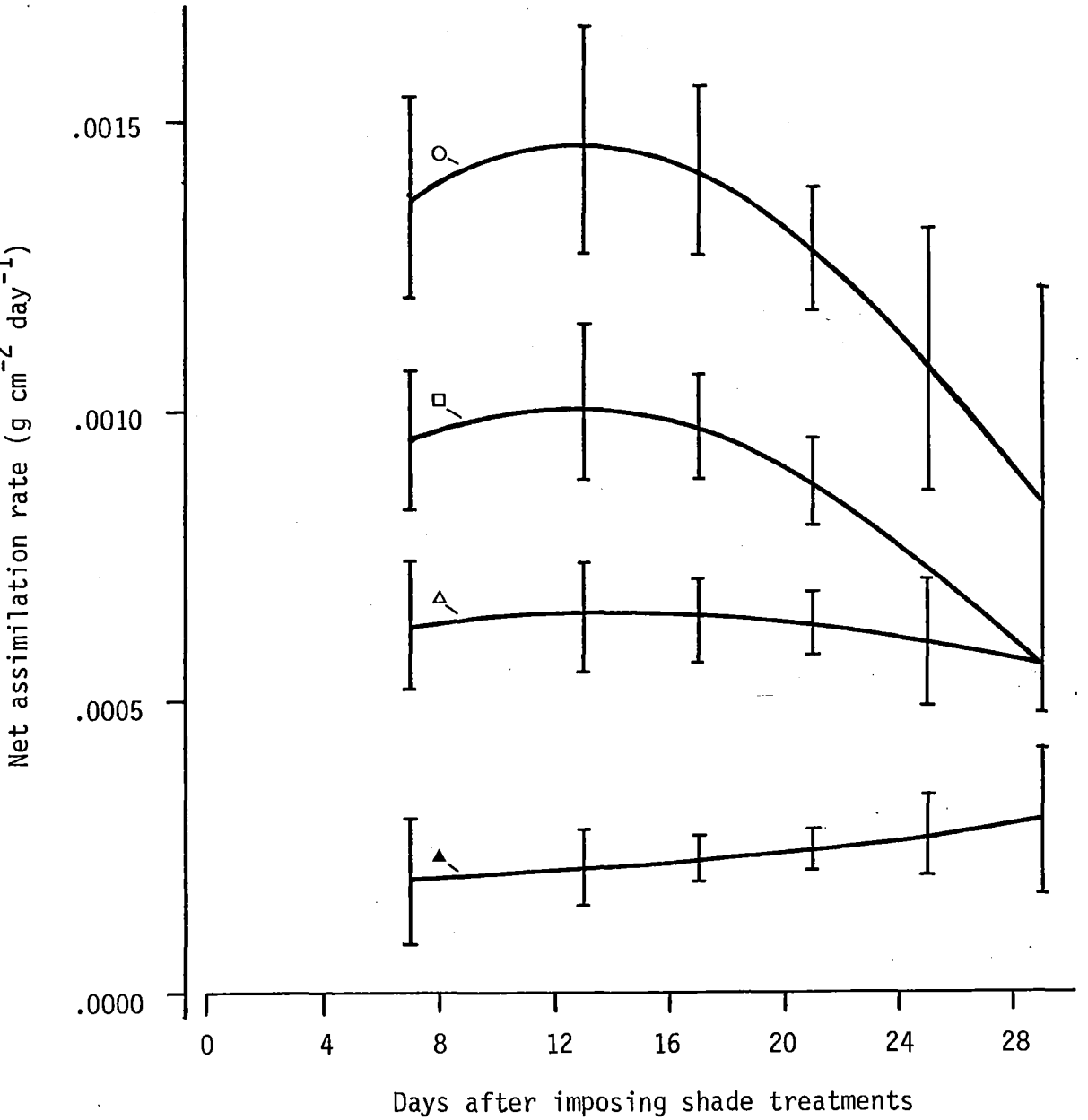


Figure 3.19 Progress curves of net assimilation rate, derived from fitted relative growth rate (Figure 3.10) and leaf area ratio (Figure 3.16) by division. Bars are the confidence limits for means of six replicate samples (95% probability). Symbols as in Figure 3.4.

When LAR was plotted against total dry weight plant^{-1} (Fig. 3.20 a) it was evident that over similar ranges in total dry weight, plants showed marked and similar ontogenetic drifts regardless of the level of shading. That is, at shading levels of 46.8, 23.7 and 6.4% full daylight, the plants initially responded by increasing their LAR until they had reached a total dry weight of 1.0 - 1.5 g, and with increasing dry weight the LARs declined at a similar rate at all light intensities. A very similar pattern was evident for SLA when plotted against dry weight (Fig. 3.20 b). This function also showed a downward drift with increasing plant dry weight at all light intensities after an initial rise to maxima at about 1.0 g plant^{-1}. On the other hand, LWR showed only slight change at dry weights above 1.5 g plant^{-1} (Fig. 3.20 c). As was the case with LAR and SLA, the drifts were similar at 100, 46.8 and 23.7% full daylight, and although LWR increased markedly up to a dry weight of 1.5 g plant^{-1} at 6.4% full daylight, it levelled out at 1.75 g and apparently would have followed a similar pattern as at higher light intensities had the experiment been continued long enough for these plants to have reached greater total dry weights.

When NAR was plotted against total plant dry weight, it was apparent that this growth function increased until the plants reached about 2.0 grams at 100, 46.8 and 23.7% full daylight, remained essentially constant between 2 and 4.5 g plant^{-1} and then declined noticeably at higher dry weights (Fig. 3.20 d). There appeared to be an interaction between light intensity and this ontogenetic drift because at 23.7% full daylight, the rate of decline of NAR was not as rapid as it was at higher light intensities, at dry weights above 4.5 g plant^{-1}. At 6.4% full daylight, NAR increased at low plant dry weights, as it did at higher light levels, and thus seemed to be following a similar pattern of change during the early stages of development.

As a consequence of these developmental changes in SLA, LWR and NAR, the RGR showed marked ontogenetic drifts (Fig. 3.20 e). At 100 and 46.8% full daylight the downward rate of changes of the RGRs as plant dry weight increased, were similar but at 23.7%, RGR did not decline so markedly as these plants increased in size, and at 6 g plant^{-1} had become greater than the RGR at 46.8% full daylight. This was the direct result of the lesser decline in NAR (Fig. 3.20 d) because LAR at this light level

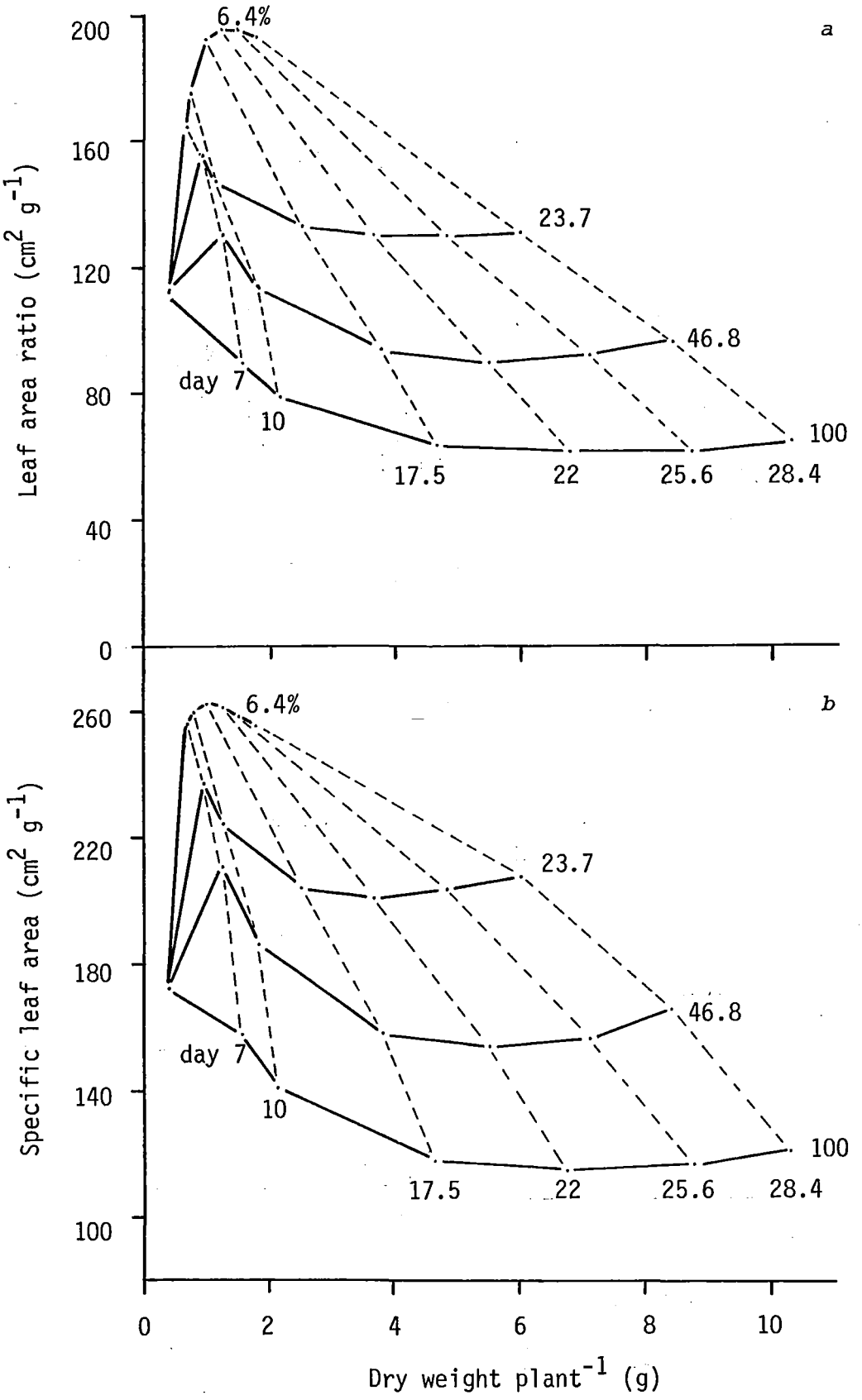


Figure 3.20 See page 83.

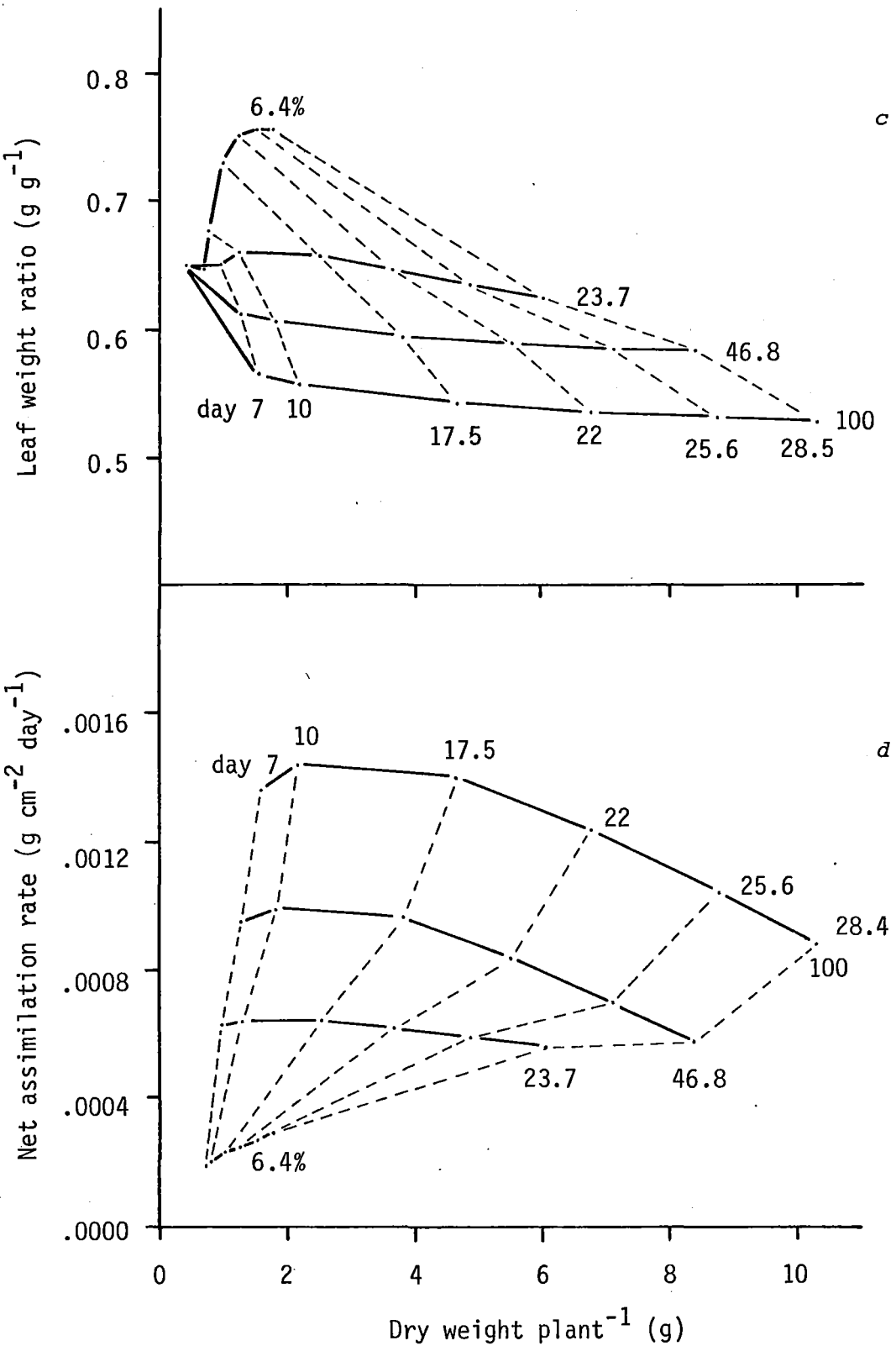


Figure 3.20 See page 83.

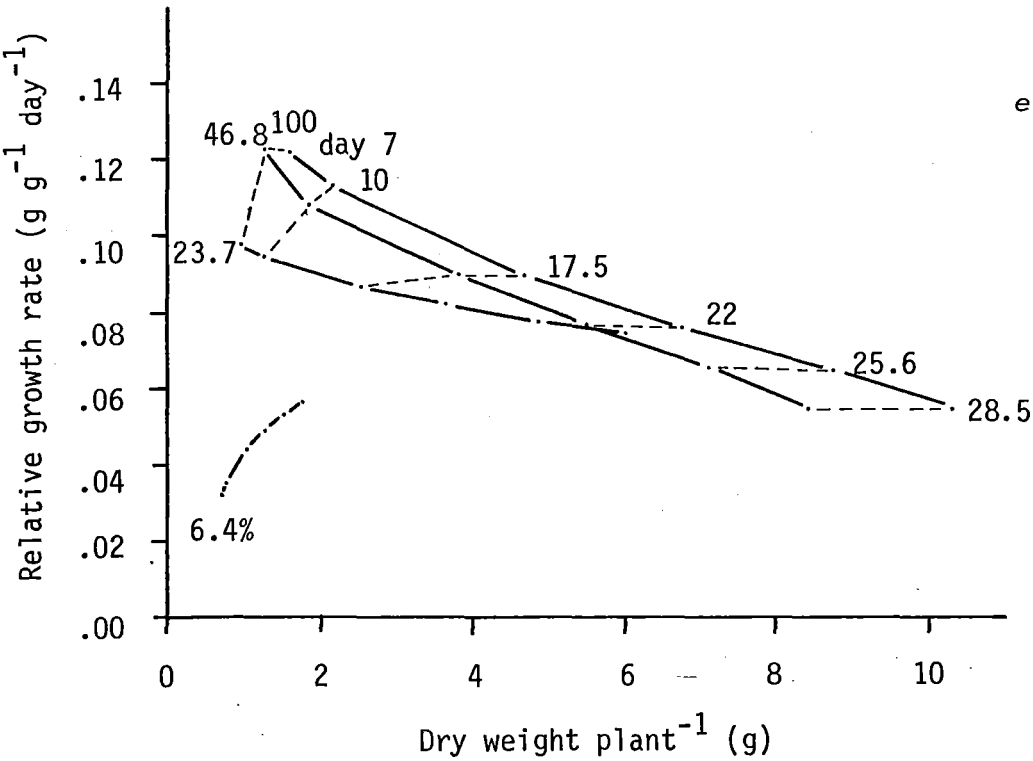


Figure 3.20 The effect of light intensity and total dry weight plant^{-1} on; *a*, leaf area ratio; *b*, specific leaf area; *c*, leaf weight ratio; *d*, net assimilation rate; *e*, relative growth rate. Dotted lines join harvests at the same time.

declined at the same rate as at the higher intensities. At 6.4% full daylight, RGR behaved quite differently, increasing steeply with increasing plant dry weight up until the maximum dry weight reached by these heavily shaded plants during the experimental period. This divergent result appeared to be predominantly the consequence of the rises in LWR (Fig. 3.20 c) and NAR (Fig. 3.20 d) as the dry weight increased in these small plants.

3.3.3 Relationships between LAR, NAR, RGR and light intensity

Linear regressions relating LAR and NAR at five points in time to log relative light intensity are presented in Fig. 3.21 and the equations for the lines are given in Table 3.7. These lines demonstrate the marked increase in LAR (Fig. 3.21 a) and the decline in NAR (Fig. 3.21 b) which occurred with increased shading. From Table 3.7 it can be seen that the LAR values (which were taken directly from the time curves in Fig. 3.16) were more closely approximated by the linear regressions with increasing time, but the converse was true for NAR (derived from Fig. 3.19). It is also clear that the slopes of these lines varied with time as a consequence of the trends with time of these growth functions (Figs. 3.16 and 3.19). Because of this, the curves relating RGR to log relative light intensity, obtained by multiplying together the linear regression estimates of LAR and NAR, varied considerably in form (Fig. 3.22). For example, the regressions fitted to LAR and NAR for day 7 predicted maximum RGR to occur at 137% full daylight, whereas for day 28 the maximum value of RGR occurred at 25% full daylight (Fig. 3.22). As a consequence of the time changes in NAR, the extrapolated estimate of the compensation point for light varied from 1.7% full daylight at day 28 to 4.6% at day 7 (Fig. 3.21 b). Due to the deviations of the LAR and NAR values from the linear regressions, the derived quadratic curves for RGR did not closely follow the RGR values predicted by the time-curves in Fig. 3.10, except at day 10 (Fig. 3.22).

When the values of LAR and NAR at a constant total plant dry weight of 1.62 g were plotted against log relative light intensity, LAR was exactly linear, whilst 98% of the variation in NAR was explained by the variation in log relative light intensity when a linear regression was fitted to this component (Fig. 3.23, Table 3.8). The extrapolated estimate

Table 3.7 The linear regression equations describing the relationship between log relative light intensity and LAR and log relative light intensity and NAR at varying times after imposing shade treatments (log relative light intensity is the logarithm of the intensity of photosynthetically active radiation (PAR) expressed as a percentage of the full daylight value).

	days after imposition of shade		
LAR	7	$Y = 227 - 62.8\,X$;	$r^2 = .862$
	10	$Y = 248 - 81.3\,X$;	$r^2 = .962$
	14	$Y = 268 - 99.0\,X$;	$r^2 = .993$
	22	$Y = 287 - 114.4\,X$;	$r^2 = .996$
	28	$Y = 281 - 109.6\,X$;	$r^2 = .999$
NAR	7	$Y = -0.0006207 + 0.000974\,X$;	$r^2 = .985$
	10	$Y = -0.0006851 + 0.001028\,X$;	$r^2 = .981$
	14	$Y = -0.0006809 + 0.001034\,X$;	$r^2 = .978$
	22	$Y = -0.0004434 + 0.000808\,X$;	$r^2 = .976$
	28	$Y = -0.0001139 + 0.0004828\,X$;	$r^2 = .943$

where Y = LAR ($cm^2\ g^{-1}$)
X = log % PAR

where Y = NAR ($g\ cm^2\ day^{-1}$)
X = log % PAR

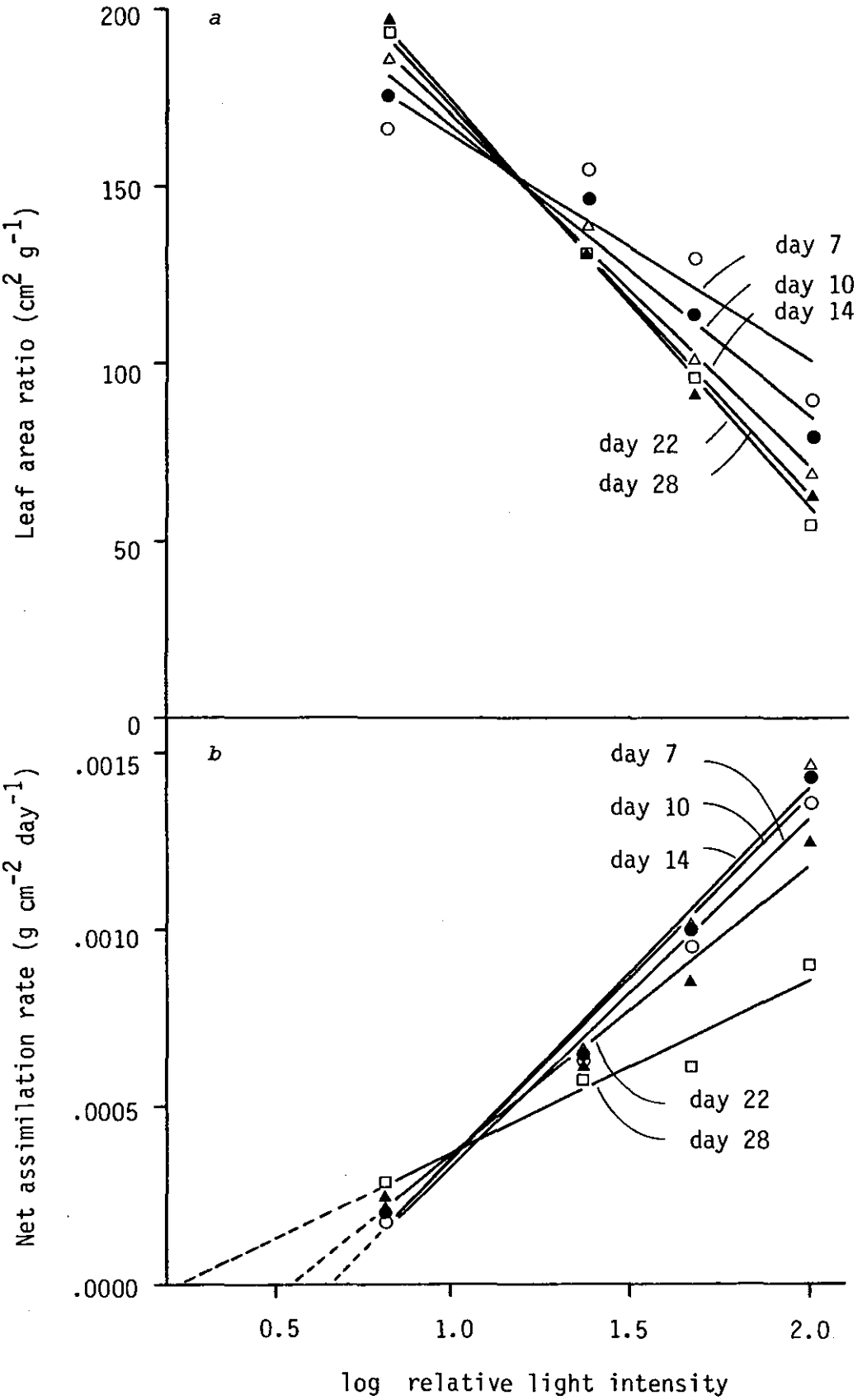


Fig. 3.21 The effect of varying light intensity on; *a*, leaf area ratio; *b*, net assimilation rate at five instants in time. Points are the instantaneous values predicted by the curves in Figures 3.16 and 3.19; lines are the linear regressions fitted to these points. Symbols as in Figure 3.22.

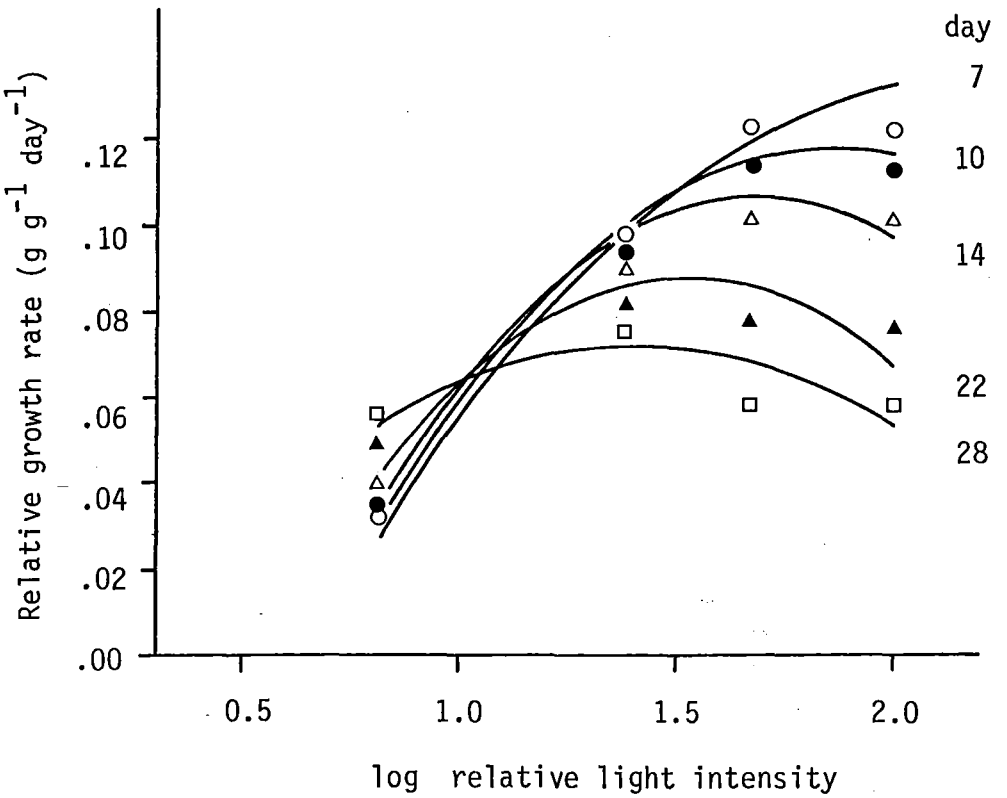


Figure 3.22 The effect of varying light intensity on relative growth rate at five instants in time. Points are the instantaneous values predicted by the curves in Figure 3.10; lines are the quadratic curves derived by multiplication of the linear curves in Figures 3.21 *a* and *b*. ○——○, day 7; ●——●, day 10; △——△, day 14; ▲——▲, day 22; □——□, day 28.

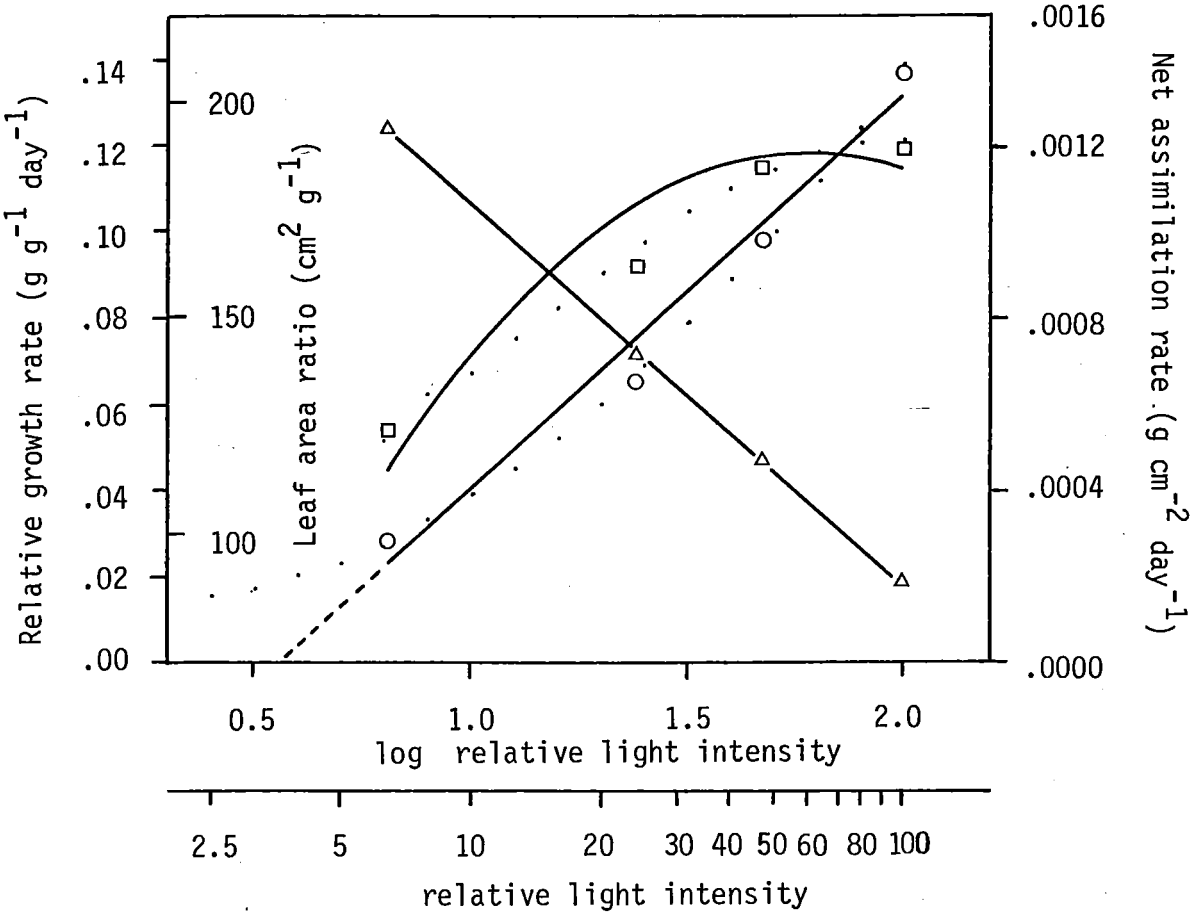


Figure 3.23 The effect of varying light intensity on leaf area ratio, △ ; net assimilation rate, ○ ; and relative growth rate, □ ; at a total dry weight plant^{-1} of 1.62 g. Points are instantaneous values predicted by the curves in Figures 3.16, 3.19 and 3.10 respectively. Straight lines are the linear regressions fitted to the LAR and NAR points; RGR curve derived by multiplication of the LAR and NAR regressions; dotted lines are the quadratic regression fitted to NAR and the derived RGR.

of the light compensation point was 3.6% full daylight and the RGR, obtained by multiplying the linear regression estimates of LAR and NAR together indicated the maximum RGR in plants of 1.62 g occurred at 59% full daylight. The RGR did not fall below its predicted value in full daylight until a light intensity of 35% of full daylight (Fig. 3.23). The RGR derived in this way closely approximated the values predicted by the curves in Figure 3.10 at 1.62 g plant^{-1} (points on Fig. 3.23), except at 23.7% full daylight where it was somewhat higher.

Table 3.8 The linear regression equations describing the relationship between log relative light intensity (see Table 3.7) and both LAR and NAR at a constant total plant dry weight of 1.62 grams.

LAR	$Y = 264.8 - 88.63\ X$;	$r^2 = .999$
	(See Table 3.7 for units of X and Y)	
NAR	$Y = -0.000504 + 0.0009061\ X$;	$r^2 = .977$

To see if a better approximation of the trend in RGR with increasing light intensity could be obtained, a quadratic regression was fitted to NAR on log relative light intensity. Although 99.9% of the variation in NAR was then explained by variation in log relative light intensity, the extra reduction in the error sum of squares due to the inclusion of the X^2 term, was not significant. On this basis, the linear regression was accepted as on adequate description of NAR on log relative light intensity. This quadratic regression for NAR and the RGR curve derived by multiplying the quadratic NAR function by the linear LAR function are given in Figure 3.23 (dotted lines) for comparison.

3.4 DISCUSSION

The RGR_W of yarrow changed with time and with the level of shading and it is now possible to discuss these changes in terms of the drifts with time in, and the treatment effects on, the physiological efficiency growth component, NAR, and the morphogenetic components, SLA and LWR. However, the interpretation of these results only in terms of shading without prior consideration to the possibility of correlation of other

environmental factors with the shading treatments would be premature and hazardous. Screens employed to reduce the intensity of light received by plants may modify the temperature of the air and root medium, air turbulence and relative humidity (Waggoner, Pack and Reifsnyder, 1959), factors which may themselves influence growth. For example, Blackman (1956) found the SLA of *Helianthus annuus* increased 50% with a temperature increase from 15 to 24^{o} C whilst Hughes (1965 b) showed with *Impatiens parviflora*, how SLA declined with a reduction in temperature below 15^{o}C. The RGR of *Dactylis glomerata* increased from 5 to 10^{o} C but declined from 20 to 30^{o} C as a result of increases and decreases respectively in both LAR and NAR (Eagles, 1971 a). This increase in LAR was associated with increases in both SLA and LWR and decreases due similarly to decreases in the latter two components. The shade houses employed in this experiment only slightly altered the temperature regime of the experimental plants. The nightly minima were up to 1.0^{o} C warmer under the shades and the daily maxima up to 2.9^{o} C cooler (Appendix XXIII). It was therefore considered that the plants at all shading levels experienced very similar temperatures and this factor was excluded as a major cause of the observed treatment effects.

Air turbulence may affect plant growth. Warren and Wadsworth (1958) suggested the increased growth of *Brassica napus* with increasing wind resulted from greater CO_2 uptake, but Wadsworth (1960) could find no changes in LAR, NAR or RGR of adequately watered *B. napus*, *Hordeum vulgare* and *Pisum sativum* plants with increasing wind. Wadsworth concluded that wind may reduce growth by causing a water shortage. On the other hand, Whitehead (1957) observed an increase in the thickness of leaves of *Zea mays* (SLA declined) after exposure to wind, resulting in reduced dry matter accumulation. Measurements were not made of the air movement through the experimental shade houses used here, but it was considered that the woven nature of the shade cloth and the gap provided around the base of the shades allowed considerable passage of air, at least sufficient to prevent CO_2 becoming limiting. However, lower SLAs in the open due to structural changes as a result of wind cannot be completely discounted. It was however assumed, that wind was not an important factor in the observed treatment effects. Furtheremore, water supply was not correlated with the treatment effects because all plants were adequately watered throughout the

experimental period.

The spectral composition of light plays an important role in plant growth (Bickford and Dunn, 1972). For example, the SLA of *Impatiens parviflora* was shown to increase with a reduction in the ratio of red to far red light (Young, 1974), a phenomenon recorded under plant canopies due to absorption of red light by photosynthesising leaves. However, the shade fabrics used here were spectrally neutral (Appendix XVIII) and therefore plants under all treatments received light of the same quality. Other unmeasured environmental variables such as soil temperature and humidity cannot be eliminated as possible causes of the observed treatment effects but it was considered justifiable to assume that the responses of the plants were largely those to reduced light intensity and hence reduced total daily irradiation.

Owing to the marked difference displayed by the RGR_W in both its magnitude, and direction of response with time at 6.4% full daylight compared to the higher light levels (Fig. 3.10), it is convenient to discuss first the effect of the latter treatments and the associated time drifts. The RGR_W at 100, 46.8 and 23.7% full daylight declined linearly with time, although more steeply at 100 and 46.8% than at 23.7% full daylight. It was apparent that these marked time drifts were the consequence of similarly marked time drifts in SLA (Fig. 3.17) and NAR (Fig. 3.19) with less marked changes in LWR (Fig. 3.18). However the drifts in these components operated at different stages in the continuing decline of RGR_W. At 100 and 46.8% full daylight LWR continued to decline throughout the experimental period (Fig. 3.18) and was thus always a component of the decline in RGR_W. However, the SLA declined rapidly in the first half of the period (Fig. 3.17) while NAR remained almost constant (Fig. 3.19), and because of the greater magnitude of this drift compared to that of LWR, the initial decline in RGR_W was mainly the result of the substantial fall in SLA. In the second half of the period, at 46.8 and 100% full daylight, the SLA approached a minimum level and then began to increase (Fig. 3.17) but the NAR was declining rapidly (Fig. 3.19) during this time and clearly was predominantly responsible for the continuing decline in RGR_W (Fig. 3.10). *Impatiens parviflora* also showed an ontogenetic drift in SLA (Evans and Hughes, 1961) which was due to an increased proportion of mature tissues in relation to meristematic tissue in the leaf and continued cell wall

thickening with age. Similar processes were probably occurring in the leaves of yarrow as the plants aged, causing the SLA to decline. As these plants became older and larger at 100 and 46.8% full daylight, and more basal second order axes were formed, the lower, earlier formed leaves became shaded by the upper leaves. It was most likely that this phenomenon of self shading lead to the rapid decline in NAR in the later stages of the experiment (Fig. 3.19). NAR has similarly been found by others to show little ontogenetic drift, remaining essentially constant until self shading begins (Blackman and Wilson, 1951 a; Evans and Hughes, 1961).

The RGR_W at 23.7% full daylight also declined with time, but much less rapidly than at 100 and 46.8% full daylight (Fig. 3.10). At this light level, NAR declined only slightly over the experimental period (Fig. 3.19) indicating that self-shading did not occur to any great extent. The decline with time in RGR_W was attributable mainly to the downward drift with time in SLA during the early stages of the experiment (Fig. 3.17) and in the later stages, to the decline in LWR (Fig. 3.18) and to a small degree, to the decline in NAR (Fig. 3.19).

At 6.4% full daylight, in contrast to the higher light intensities, the RGR_W increased with time throughout the experimental period. This was the result of the upward drift in LWR (Fig. 3.18) and a slowly increasing NAR (Fig. 3.19), the SLA remaining almost constant (Fig. 3.17).

Whether these marked drifts with time in RGR_W are entirely attributable to ontogentic drifts in SLA and LWR, and not partially the result of seasonal changes in environmental factors is debatable. The best way of resolving this question would be to eliminate seasonal changes by growing plants in constant conditions in controlled environment growth cabinets. However, this field experiment ran for less than one month in the summer, during which time major environmental factors likely to affect SLA, LWR and NAR showed no trends (Appendix XIX). It is therefore suggested that the drifts in SLA and LWR, so clearly evident in the continuous time traces derived from the regression analysis, were almost entirely ontogenetic.

When yarrow was shaded to 46.8% full daylight, the RGR_W showed a striking resilience and remained almost unchanged from the value in full

daylight (Fig. 3.10), despite the reduction in NAR (Fig. 3.19). This tolerance of shading was the result of the remarkable adaptability of the LAR which was increased at 46.8% full daylight to a level which entirely compensated for the decline in NAR (Fig. 3.16). It was apparent that this modification of the LAR was brought about by both an increase in the expansion of the leaf tissue (increased SLA, Fig. 3.17) and by a greater percentage commitment of total plant dry matter to leaf tissue (increased LWR, Fig. 3.18), although the relative change in LWR was less than that of SLA. The SLA is well known to be a highly plastic growth function in response to shading (Evans and Hughes, 1961; Coombe, 1965; Hughes, 1965; Hurd and Thornley, 1974), but LWR often proves to be quite stable plants tending to maintain their proportioning of total dry weight in leaf tissue over a wide range of light intensities (Blackman, 1956; Evans and Hughes, 1961). Yarrow, in contrast, appears to show adaptability of both these components of leafiness. At 23.7 and 6.4% full daylight, the SLA and LWR, although still showing considerable adaptability, were unable to completely compensate for the reduction in NAR (Fig. 3.19) and therefore the RGR_W was reduced (Fig. 3.10).

The rapidity with which these adaptational changes in LAR and the reductions in NAR took place were of some importance. The plants in all treatments began at the same total dry weight, but despite this and even though the RGR_W was the same at 46.8 and 100% full daylight throughout the period of measurement (Fig. 3.10), the total dry weight $plant^{-1}$ was reduced at 46.8% full daylight (Fig. 3.9). This can only be explicable by the RGR_W having been lower at 46.8% full daylight during the first 7 days of shading. This was most probably due to an immediate reduction in the NAR upon shading, and a delay in the adaptation of the LAR to the reduced light. Evans and Hughes (1961) suggested that the adaptation of LAR of *Impatiens parviflora* was slow in contrast to the rapid reduction in NAR with shading (Hughes, 1965 b); LAR became fully adapted in young plants after 7 days. The time taken for complete adaptation of LAR to 46.8% full daylight in yarrow cannot be stated with certainty, but it seems clear that full adapatation had substantially occurred within the first 7 days of shading because RGR_W had returned to its rate in full daylight by the first harvest (Fig. 3.10).

In order to assess the response of the RGR_W of yarrow to reduced light and to allow a tentative comparison with other species, the techniques of Blackman and Wilson (1951 b) were employed. These authors defined a shade tolerant species as one with a large capacity to increase its LAR when shaded, from an initial low level in full daylight. In this way the plant is able to compensate for reduced NAR down to lower light levels than plants with less adaptable LAR, and can therefore produce dry matter more efficiently at low light intensities than can less adaptable plants.

Linear regressions were fitted initially to instantaneous values of NAR and LAR for several points in time during the experimental period (Fig. 3.21 a and b), and the RGR_W was derived by multiplication (Fig. 3.22). It was immediately apparent that the ontogenetic drift in LAR and the decline in NAR with self shading, profoundly altered the form of the derived quadratic curves of RGR_W (Fig. 3.22), so that an ecological interpretation would be dependent upon the choice of curve. At successively later stages in the experiment, the light intensity at which RGR_W was maximal became lower, from a value in excess of full daylight at day 7 to about 25% full daylight at day 28. Similarly, when the NAR regressions were extrapolated to the light axis to estimate the compensation point for light (a hazardous process, assuming the continuation of linearity), the predicted values at which growth would stop ranged from 4.6% full daylight at day 7 to 1.7% at day 28 (Fig. 3.21 b). For a more meaningful comparison of the treatment effects, it was desirable that they were compared on a basis which took account of the ontogenetic drifts in LAR. It was considered that a way of doing this was to replot the growth functions against total plant dry weight, assuming that dry weight was a better measure of physiological age than was chronological time (Evans, 1972, 1976, and Eagles, 1971 a). When this was done, it appeared that plants of the same total dry weight, were progressing through sim ilar ontogenetic drifts of LAR (Fig. 3.20 a). Thus although the LAR at 6.4% full daylight rose rapidly with time to a maximum, followed by a fall in the final stage of the experiment (Fig. 3.16), contrasting mardkedly with the time drifts at higher light levels, when plotted against total plant dry weight, it was seen that the drifts were very similar at all light intensities. The LAR increased to a maximum at between 1.0 - 1.5 grams $plant^{-2}$, as

adaptation to the new light levels took place, and then began to fall at a similar rate at all light intensities (Fig. 3.20 a). Thus it would appear that the considerable difference in the progress of LAR on time at 6.4% full daylight, compared with that at higher intensities was the result of the retardation of ontogeny at this low light level. Similar, but less marked retardation occurred at the other light intensities of less than full daylight. Evidence of developmental retardation is not only apparent in the small size attained by the heavily shaded plants (Figs. 3.20 a; 3.9; 3.15 b), but is also clear from the considerably reduced flower stem formation at 6.4% full daylight (Table 3.6). Similarly, it is suggested that developmental retardation with increased shading was the cause of the different time drifts of SLA (Fig. 3.1) and LWR (Fig. 3.18) because when these were plotted against dry weight (Figs. 3.20 b and c), they also appeared to be changing in similar ways at all light levels as total dry weight increased. It is therefore argued that had the experiment been continued for a longer period, allowing the heavily shaded plants (6.4% full daylight) to increase in total dry weight, i.e. become developmentally more advanced, then the SLA and LWR curves (Figs. 3.20 b and c) would have declined with increasing plant dry weight at the same rate as at higher light intensities.

When NAR was plotted against total plant dry weight, there appeared to be a slight increase with age up to 1.0 gram plant^{-1} (Fig. 3.20 d), but it then remained essentially constant until 4.0 to 4.5 grams plant^{-1} when it declined rapidly with increasing total dry weight as a result of self shading. At 23.7% full daylight however, in contrast to higher light intensities, the NAR did not fall noticeably, and at 6.0 grams plant^{-1} was only marginally less than at 1.0 gram plant^{-1}. The most plausible explanation for this was that the structural changes in the leaves (Fig. 3.5) and their different spatial arrangement, especially the more erect habit (Fig. 3.15 b) at this low light intensity allowed these plants to reach greater total dry weight before self shading began. It was this phenomenon which caused the RGR_W at 23.7% full daylight to fall less steeply with increasing plant dry weight so that at 6 grams total dry weight plant^{-1}, these plants were growing as efficiently as those at 46.8% full daylight (Fig. 3.20 e).

If as the data suggest, the SLAs and LWRs of the plants at all light intensities were passing through similar ontogenetic drifts, drifts which were obscured when the functions were plotted against time, then assessment of the treatment effects at a constant time after the beginning of shading confounds these effects with the ontogenetic changes. In order therefore, to arrive at a more meaningful appraisal of the effects of shading, i.e. meaningful in terms of the plants stage of ontogeny, total dry weight was chosen as the basis for the comparison. The relationships between both LAR, NAR and the logarithm of the relative light intensity were established at a constant total plant dry weight of 1.62 grams plant^{-1}. Following the procedures and assumptions of Blackman and Wilson (1951 b), the response of the RGR_W was secured, and the light intensity at which maximum RGR_W occurred (59% full daylight) was calculated as the light intensity midway on the logarithmic scale, between the LAR extinction and NAR compensation points (Fig. 3.23). From these results a tentative assessment can be made of the shade tolerance of yarrow seedlings and the mechanisms whereby they may tolerate a wide range of light intensities. It should be noted that the conclusions to be drawn from this analysis apply only to plants at a total dry weight of 1.62 grams for it will be apparent that the continuing downward drift of LAR with increasing dry weight (Fig. 3.20 a) would cause the LAR relationship to become displaced further below its present position. Thus the maximum RGR_W would become lower and would also occur at progressively lower light intensities as the LAR extinction point declined. The curve would become flatter so that RGR_W would be relatively stable over a wider and wider range of light intensities. As NAR fell with time, the extrapolated estimate of the light compensation point would increase tending to further lower the maximum RGR_W and cause it to be maximal at higher light intensities. Such alterations in the estimate of the point of maximum RGR_W, due to drifts with time in LAR and NAR have been mentioned by Jarvis (1964).

The growth of yarrow in full daylight was high and it responded to shading by a remarkable increase in the expansion of its leaf surface, and by committing a greater proportion of its total dry matter to leaf tissue. The combined effect was a steep rise in the LAR with increased shading (Fig. 3.23). The fall in NAR (Fig. 3.23) was at first more than

offset by the increased leaf surface, so that the maximum RGR_W was found at 59% full daylight; in heavy shade (6.8% full daylight) the NAR was reduced to 19% of the value in full daylight but the RGR_W was only reduced to 42% of its full daylight value (Table 3.9). Fenner (1978) found yarrow seedlings were the most shade tolerant of a number of closed-turf species occurring in relatively dense grassland situations. The mean RGR of yarrow over a five-week period at 6.8% full daylight was 47% of the value in full daylight whereas other closed-turf species suffered a greater relative reduction in their mean RGRs over the same period. The results presented here have fully substantiated Fenners observations on yarrow but go further in showing just how this tolerance of shade is achieved. Grassland species also tend to show shade avoidance mechanisms which allow them to locate their leaves above the zones of low light intensity in the lower parts of swards (Grime and Jeffrey, 1965). Fenner (1978) found that shaded yarrow seedlings displayed a shade avoidance mechanism by extending the length of the leaves and concluded that in a grassland situation, this mechanism would be of importance in the establishment and growth of yarrow seedlings. This mechanism was also demonstrated in this experiment where leaves were considerably longer when shaded (Fig. 3.5) and grew almost vertically upward in the heavily shaded treatment (Fig. 3.15 b).

An accurate estimate of the light compensation point could not be made, but it is undoubtedly very low as the extrapolated linear regression of NAR on the logarithm of the relative light intensity intercepted the light axis at 3.6% full daylight (Fig. 3.23). Although the light intensities in the lower half of grass/clover swards may fall as low as 5% of full daylight or less (Stern and Donald, 1962), approaching the level where yarrow would stop positive growth, avoidance of these low intensities by vertical leaf elongation would allow continued growth of yarrow. It is suggested that this avoidance mechanism and the considerable shade tolerance owing to the morphogenetic adaptability are important biological features permitting yarrow to survive in grassland and tall grass-weed roadside communities. Light measurements beneath cereal crops have indicated that at the time of maximum canopy formation, the light intensities are often greater than the estimated compensation point of yarrow (Bula, Smith and Miller, 1954; Klebesadel and Smith, 1959;

Table 3.9 Comparison of effects of shading on yarrow and other species. (Figures in brackets are the values expressed as a percentage of the full daylight value).

	NAR	LAR	RGR
	$g\ cm^{-2}\ day^{-1}$	$cm^2\ g^{-1}$	$g\ g^{-1}\ day^{-1}$
Helianthus annuus (Blackman and Wilson, 1951 b)			
% Daylight			
100	.00114	82	.094
24	.00041 (36%)	140 (171%)	.060 (64%)
12	.00019 (17%)	170 (207%)	.033 (35%)
Impatiens parviflora (Evans and Hughes 1961)			
% Daylight			
100	.00086	132	.114
24	.00047 (54%)	239 (181%)	.111 (97%)
12	.00029 (33%)	315 (239%)	.090 (79%)
Achillea millefolium			
% Daylight			
100	.00131	88	.115
24	.00075 (57%)	142 (161%)	.107 (93%)
12	.00047 (36%)	169 (192%)	.079 (69%)
6.8	.00025 (19%)	191 (217%)	.048 (42%)

Skuterud, 1977), although Stahler (1948) showed that the light intensity beneath rye (*Secale cereale*), oats (*Avena sativa*) and soybeans (*Glycine max*) may fall below this estimate. Consequently, even though considerable reduction in the growth of yarrow beneath crops would be expected, it is unlikely that complete cessation of growth would occur, providing nutrients and water were not limiting. Even if light levels beneath an annual crop were to fall below the compensation point, food reserves within the rhizome system would be likely to ensure survival until light levels improved as the crop canopy senesced. The ability of seedlings without rhizomes to withstand a period with light intensity below the compensation point may be less than for plants with a rhizome system, such as those regenerating from fragmented rhizomes.

Table 3.9 compares the performance of yarrow in this experiment, at a total plant dry weight of 1.62 grams with that of the well-known sun plant, *Helianthus annuus* (Blackman and Wilson, 1951 b, data from their Fig. 7, period 2) and with the facultative shade plant, *Impatiens parviflora* (Evans and Hughes, 1961, data from their Fig. 6). It is clear that *Helianthus annuus* shows a marked fall in NAR with shading which is only partially offset by increased LAR, giving poor overall growth in the shade. In contrast, both *Impatiens parviflora* and *Achillea millefolium* showed lower percentage reductions in NAR so that their RGRs were relatively less reduced by shading. The responses of the LARs were similar in all three species, contrary to the definition of shade tolerance proposed by Blackman and Wilson (1951 b), and Jarvis (1964) where emphasis was placed on the increase in LAR upon shading, relative to its value in full daylight. The shade tolerance of a species depends upon its ability to continue to efficiently produce dry matter at light intensities less than full daylight and this is clearly affected by both the responses of NAR and LAR to the shading.

Although yarrow does not form natural communities in dense shade, it does occur in a wide range of light environments, from open cultivated fields, where growth and rhizome production can be extremely vigorous, to grasslands, roadside weed communities and in a number of arable crops (Bourdôt, White and Field, 1979) including the cereals. It is considered that the ability to avoid deep shade at the base of the communities by leaf extension and vertical orientation, the formation of tall leafy

flower stems, the marked morphogenetic adaptability bestowing considerable tolerance of shade, and the undoubtedly low compensation point are biological features of great importance to the survival and growth of yarrow in grasslands and in the wide range of arable crops in which it occurs. It is concluded that yarrow is not a high-light-demanding species.

CHAPTER 4

COMPETITION BETWEEN YARROW AND BARLEY AND THE SUBSEQUENT GROWTH OF YARROW DURING THE AUTUMN AND WINTER

4.1 INTRODUCTION

The competitiveness of yarrow toward sown crops has been commented upon in the literature. Hilgendorf and Calder (1952) stated that yarrow was a serious weed on arable land, as it often grew so densely as to choke out cereal and other crops, and Saxby (1944) considered the plant as a bad weed on arable land on account of the competition with sown crops. Reynolds (1961) remarked that yarrow was not deterred by vigorous competition from other species (presumably pasture species) that flourish on high fertility soils, especially in the lower rainfall areas where its relative drought resistance apparently confers a competitive advantage over less resistant species. Increase and success of yarrow in high fertility pastures has also been demonstrated by other workers (Hay and Ouellette, 1959; Haken, 1968; Habvostiak, 1973). However, there is some evidence that suitably competitive annual crops may play an important role in a control programme for yarrow on arable land. Connell (1930) in discussing the control of 'twitchy' perennial weeds (including yarrow), suggested that a 'suitable' rotation spread over a number of seasons, and which always pays its way, rather than expensive summer fallow should be followed to achieve control of these plants. Summer fallow cannot be relied upon for complete control of yarrow not only because of the vagaries of the weather, but also because of the brittleness of the rhizomes and the consequent difficulty of bringing all regenerative tissue to the surface where it may be desiccated (Hilgendorf and Calder, 1952). Therefore Connell (1930) advocated augmenting the weakening effect of summer fallow by sowing immediately a dense and quick-growing cereal crop which it is presumed, would bring about the demise of the yarrow population. Hilgendorf and Calder (1952) also suggested that control could be effected by sowing a heavy smothering crop, for example, oats (*Avena sativa*) and tares (*Vicia faba*) after summer working to reduce the population. There have however, been no scientific investigations of competition in a crop/yarrow association and there is consequently no data

which demonstrates either the magnitude of any crop losses caused by the presence of yarrow, or the degree to which a smothering crop may reduce the growth of yarrow.

There is some evidence to suggest the growth of yarrow may not be restricted to the warmer months. For example, for the sowing of oats and tares in the autumn to effect control of yarrow, then active growth during the months when the crop is present, i.e. autumn and winter, must be occurring. The growth pattern of yarrow in New Zealand has not been the subject of study, but in a reply to A.H. Rowe in 1924, the Department of Agriculture suggested that autumn growth of yarrow may be greater than that of lucerne (*Medicago sativa*), hence making it essential to eradicate the plant before autumn sowing of the crop to prevent vigorous competition from the yarrow during the establishment phase. The literature available thus suggests that yarrow is winter active in New Zealand but the extent of this activity and the relative rates of growth of aerial shoots and rhizomes has not been reported.

In view of the potential importance of crop competition in a programme for yarrow control/eradication, and the significance of active winter growth, should it occur, in the planning of such a programme, the experiment reported in this Chapter was carried out. The experiment is in two parts which relate to the following two primary objectives:

1. To determine the intensity of interspecific competition between low populations of yarrow regenerating from planted rhizome fragments, and a spring-sown barley crop.

2. To investigate the extent of growth and development of pure yarrow populations and of those in the stubble of the barley during the autumn and winter.

4.2 MATERIALS AND METHODS

4.2.1 Experimental procedure

A split plot design experiment was laid out on a Wakanui silt loam on the Lincoln College Research Farm. The site was yarrow-free and had previously grown barley. The main plots were arranged in six randomised blocks with treatments as in Table 4.1.

Table 4.1 Yarrow and barley treatment combinations

	Yarrow	Barley
1	none	low population
2	none	high population
3	low population	none
4	low population	low population
5	low population	high population
6	high population	none
7	high population	low population
8	high population	high population

For yarrow, the low population was achieved by planting 25 10 cm rhizome pieces m^{-2} while the high population was obtained by planting 50 10 cm pieces m^{-2}. The low population of barley was secured by sowing 91 kg viable seed ha^{-1} while 168 kg was sown to obtain the high population.

Each main plot measured 2.7 m x 12.0 m, with a central strip, 1.0 m wide, planted with yarrow where required and the whole plot drilled with barley. Rhizome fragments, 10 cm long, (with a mean dry weight of 0.15 g), unbranched and with undamaged buds were selected from a natural stand growing nearby on the same soil type. They were planted with the aid of a planting device (Appendix XX) at a uniform depth of 5 cm, in rows of five running across the plots, with 10 cm between the ends of each piece. The two densities were achieved by planting the rows at 10 or 20 cm apart down the plots.

The subplot factor, harvest times, was provided for by allocating the numbers one to ten, to ten harvest positions. The positions were marked out with wire pegs 40 cm apart, while planting the rhizome pieces, which occupied the central 4 m of each plot.

The yarrow was planted on 4 and 5 November 1977 into barley which had been drilled on 3 November. However the barley had to be redrilled on 29 November as a result of severe barley damage caused by terbutryn which had been sprayed to control wireweed (*Polygonum aviculare*). Subsequently weeds were removed by hand as they emerged.

All plots received an application of a compound fertiliser contain-

ing N.P.S. in the ratio of 7: 5: 14:, at the rate of 399 kg/ha. The trial was irrigated by overhead sprinklers giving 50 mm on 11 November, 25 mm on 10 January and 50 mm on 21 January.

Five harvests were taken at 17 day intervals during the growth of the barley crop, beginning on 17 December 1977. This was achieved using an open ended, 20 x 60 cm ($0.12M^2$) quadrat, which was slid into the barley stand at the randomly selected positions. Four rows of barley were pulled and the yarrow, including rhizomes, was removed from the same area. This meant that three rhizome pieces and their shoots were recovered for the low yarrow density and six pieces for the high density. It also meant there was a 20 cm strip of plot left undisturbed between harvest positions.

The yarrow plants in each sample were separated into leaves, flower stems, rhizomes and capitula when present, and after measuring the total leaf area on a Li-cor area meter, the oven-dry (85^oC) weights of the components was recorded. The numbers of flower stems and their height above the planted rhizome fragments, and the total numbers and total length of the rhizomes were also recorded at each harvest. At each of the five harvests, 20 barley plants were taken as a subsample from each sample and separated into leaves and stems before measuring the leaf area and dry weights of the components. The height of the barley was measured at each harvest from soil level to the base of the youngest fully expanded leaf. After harvest 5, the grain yield of barley and its components were estimated from a subsample of 20 ears selected at random from a sample taken on 13 March 1978 which comprised of the 5 remaining 0.12 m^2 sample positions. The barley, along with any yarrow stems was cut with hand shears 12 cm above the soil.

The light intensity at soil level beneath the barley crop and 20 cm above the canopy was measured with an Evans Electroselenium Lightmaster Photometer. Ten replicate pairs (above and below the canopy) of measurements in each barley plot of two replicates were made on 4 January 1978, between 11.00 a.m. and 12.00 noon during which time calm and overcast conditions persisted.

The yarrow remaining on the 5 subplots from which the barley had been removed, and on the unsampled subplots of the yarrow - no barley treatments was harvested sequentially during the autumn and winter at

intervals of 34, 34, 61, 36, and 32 days. The final harvest was taken on 8 September 1978, just before the flush of spring growth. The same measurements as described above were made on the yarrow, excluding senescing stems, cauline leaves and floral parts which were included in the total dry weight as dead matter.

4.2.2 Analytical procedure

The course of interference between barley and yarrow, and the subsequent growth of the yarrow during the autumn and winter, was assessed using the techniques of growth analysis. In order to assess the changes with time in the relative growth rate (RGR) and its components, leaf area ratio (LAR) and net assimilation rate (NAR), a regression method, which is fully described in Appendices I and II, was employed. This method allowed continuous time-trends of the growth analysis parameters to be estimated, so that the final outcome of interference between the species could be understood in terms of the time varying changes in the morphological characters, specific leaf area (SLA) and leaf weight ratio (LWR) and the physiological character, NAR.

4.3 RESULTS

4.3.1 Relative times of emergence and plant number

The experiment was designed to simulate the conditions associated with normal farm practice, by planting the yarrow rhizomes along with the barley seed. Barley plants began emerging on 20 November and had produced approximately 2 to 3 leaves before yarrow shoots began to emerge in December. However, the relative times of emergence of the two species was reversed with the resowing of the barley crop; barley plants began emerging on 5 December into the stand of small yarrow rosettes.

Analysis of variance, with harvest date as the subplot factor, was carried out on the yarrow primary vertical shoot number and the barley plant number. The results of this analysis showed there was a significant trend with time in the yarrow shoot numbers. It is apparent in Table 4.2a that this was due to a delay in emergence of the yarrow shoots in the presence of both densities of barley. However, from the time of second harvest (3 January), the populations of yarrow shoots did not vary with

Table 4.2 – Yarrow and barley populations as affected by time and density of the associate species.

a) Yarrow primary vertical shoot number m^{-2}

	Harvest Date					Mean over time and barley density
	17 Dec.	3 Jan.	20 Jan.	6 Feb.	23 Feb.	
low yarrow density,						
no barley	43.1	37.5	34.7	29.2	38.9	
low barley	29.2	43.1	41.7	37.5	41.7	37 (36)
high barley	34.7	33.3	37.5	41.7	33.3	
high yarrow density,						
no barley	70.8	76.4	77.8	80.6	73.6	
low barley	56.9	75.0	70.8	75.0	65.0	70 (34)
high barley	52.8	77.8	66.7	62.5	75.0	

S.E. (Mean) for vertical comparisons 4.92

S.E. (Mean) for horizontal comparisons 3.30

Values in parenthesis are shoot numbers expressed as a percentage of the number of viable buds planted i.e. 102.5 and 205 buds m^{-2} at low and high density plantings respectively.

b) Barley plant number m^{-2}

						Mean over time and yarrow density
low barley population,						
no yarrow	188	246	210	206	218	
low yarrow	160	144	201	207	201	194
high yarrow	167	186	158	229	188	
high barley population,						
no yarrow	344	375	401	411	371	
low yarrow	360	283	350	332	365	359
high yarrow	401	390	325	350	332	

S.E. (Mean) for vertical comparisons 30.9

S.E. (Mean) for horizontal comparisons 21.4

barley density or with time and therefore the means over time and barley density, for each level of yarrow were taken as the estimates of the mean yarrow population densities; 37 and 70 primary shoots m^{-2} (Table 4.2 a).

There was no significant effect of time or of yarrow density on the number of barley plants as can be seen in Table 4.2 b. These were therefore averaged over time and yarrow density to provide an estimate of the mean number of barley plants arising from the two sowing rates; 194 and 359 plants m^{-2} (Table 4.2 b). These results show that there was no mortality in any of the barley or yarrow populations during the course of the experiment.

The mean number of buds per planted rhizome fragment was 4.1, giving 102.5 and 205 buds m^{-2} at the low and high densities of yarrow respectively. Using these values, the percentage of planted buds which produced shoots was approximately 35 to 36 (Table 4.2 a). The remaining buds were either non-viable to begin with, or were lost as a consequence of decay of the ends of the rhizome fragements, or were viable, but suppressed by the apical domiance of the developing shoot system. No record was kept of the fate of these buds which did not form shoots, but it was apparent, throughout the experiment, that a considerable proportion remained viable. The inhibited buds did not at any stage form new primary aerial shoots, although a number did grow out to form rhizomes during the later stages of the experiment.

The mean dry weight of the planted rhizome fragments was 0.15 g or 3.75 and 7.5 g rhizome dry matter m^{-2}, equivalent to field infestations of 37.5 and 75 kg ha^{-1}. Such infestations could be considered relatively low on arable land. Populations with ten times this amount of rhizome have been measured by the author.

The thousand grain weight of the barley was 46.7 g and the sown weight of viable barley seed was 9.1 and 16.8 g m^{-2} or 91 and 168 kg ha^{-1} for the low and high seeding rates respectively. The barley populations therefore had an initial advantage over the yarrow populations in having both greater numbers of individuals and a larger initial biomass, although the initial weight growing $plant^{-1}$ was greater in yarrow than barley.

4.3.2 The growth of yarrow and barley in association

The polynomials of adequate fit to the logarithms of total plant

(excluding roots) and leaf dry weight and total leaf area m^{-2} for yarrow and barley were calculated, following the procedures in Appendices I and II. Similarly, curves were also fitted to the dry weights of yarrow rhizome and flower stems, but only from day 59 (harvest 2) because rhizome and flower stems had not been formed on many plots until this time. There was no overall interaction between yarrow and barley density with respect to these growth components (Appendices VI and IX) and neither were there any interactions between the species with regard to the trends with time (Appendices VII and X). Therefore, as the prime concern was to analyse the effect of barley density on the growth and development of yarrow, and *vice versa*, the mean of both densities of each species was used for assessing the effect of the other species.

4.3.2.1 Total dry weight Barley markedly suppressed the accumulation of dry matter by yarrow (Fig. 4.1 a), but the dry matter accumulation of the barley was only slightly reduced in the presence of yarrow (Fig. 4.1 b). It is evident that dry matter accumulation continued in the yarrow populations at both levels of barley, but the difference between the populations with and without barley became greater with time; by day 110 (23 February), the total dry weight of the yarrow at 194 barley plants m^{-2} was only 9% of that without barley and it was reduced to 6% with 359 barley plants m^{-2}. In contrast, the total dry weight of the barley was suppressed to only 97% by yarrow at the low density, and to 90% at the high density.

The progress with time of the logarithms of total dry weights of yarrow and barley (observed means given in Appendices V and VIII) were adequately described by cubic polynomials. The equations for these growth curves are given in Table 4.3 and the curves are illustrated in Figure 4.2. It can be seen that the dry weight of yarrow had not been significantly reduced by day 42 (17 December) but from day 59 (3 January), the total dry weight was significantly reduced by barley at 194 plants m^{-2}, and was further significantly reduced by barley at 350 plants m^{-2} (Fig. 4.2). The total dry weight of the barley was slightly, but consistently reduced in the presence of yarrow and it is evident that the reduction was significant during the early and middle part of the growth period at the low yarrow density and significant during the middle and later part of the growth period at the high density. The barley growth curve was fitted

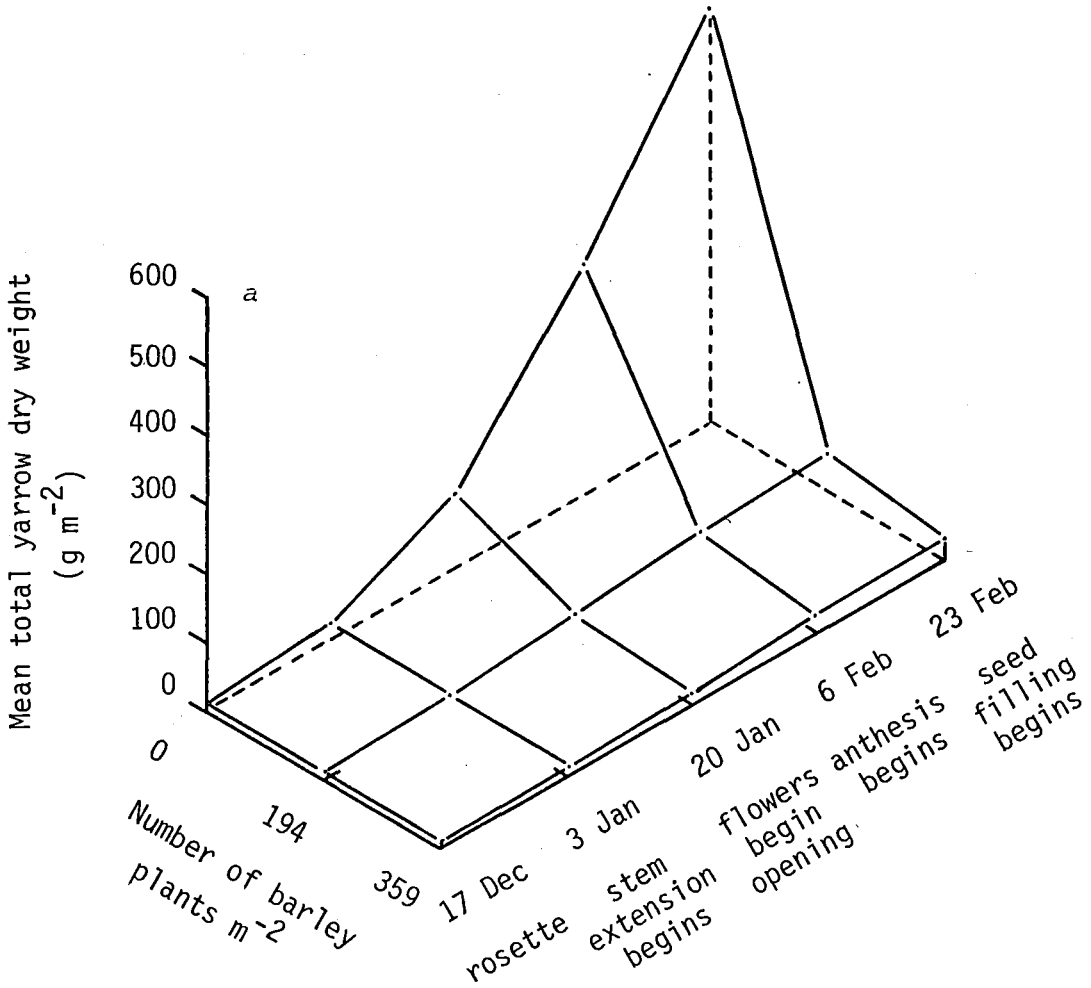


Figure 4.1 See page 110.

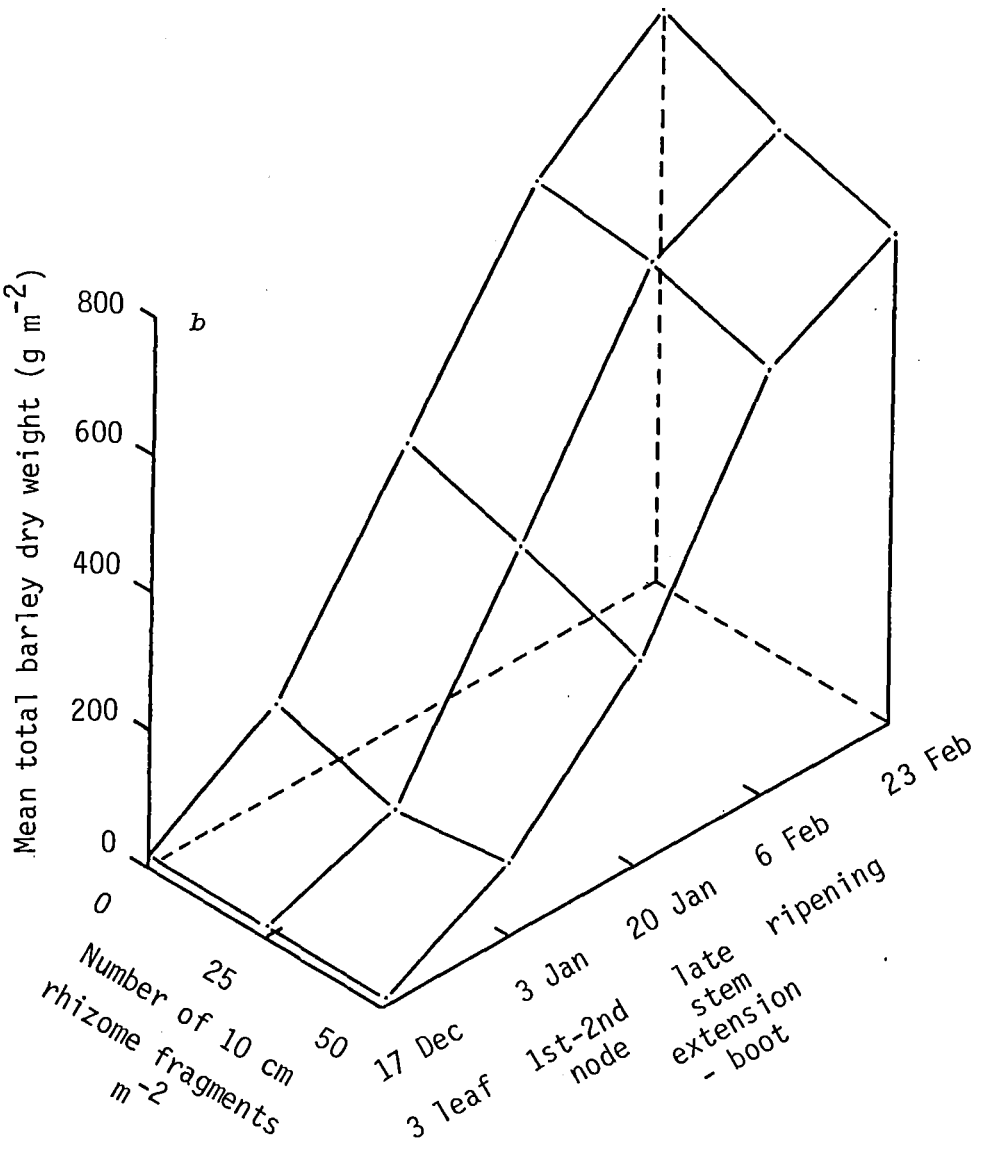


Figure 4.1 The relationship of total dry weight of yarrow and barley m^{-2} to time and density of the other species. *a*. Yarrow. Values are the backtransformed observed means of the logarithms for both yarrow densities; the means of 12 samples. *b*. Barley. Values are the backtransformed observed means of the logarithms for both barley densities; the means of 12 samples.

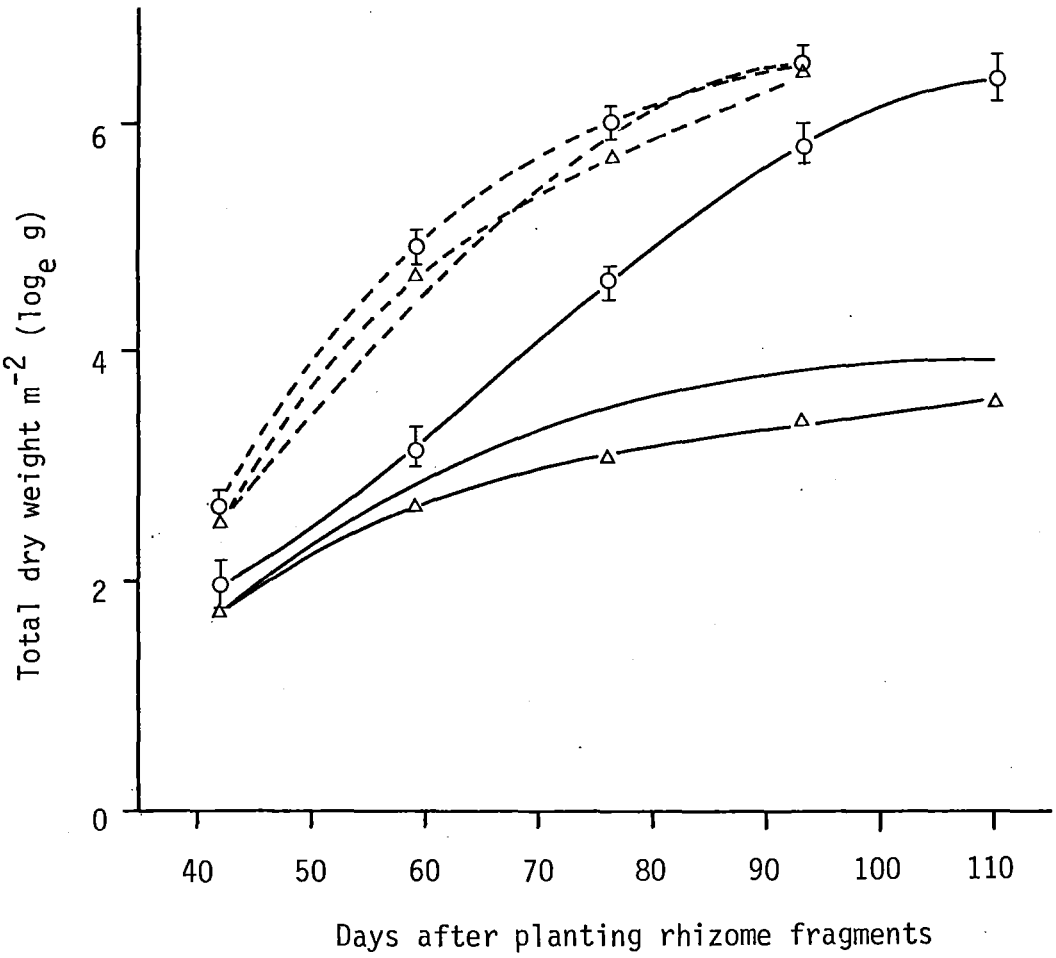


Figure 4.2 Progress curves of total dry weight m^{-2}. The points are the observed means of the logarithms for both densities of the species; means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves in each barley and yarrow set. o-----o, - - - - - ,Δ- - - -Δ, represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively. o——o, —— ,Δ—Δ, represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

only up until day 93 (6 February) because by the time of the final harvest, all leaves had senesced causing the leaf area ratio (LAR) and the net assimilation rate (NAR) to be zero.

Table 4.3 Regression equations for $\log_e$ total dry weight m^{-2} (W). t in days from planting rhizome fragements; W in g.

barley density (plants m^{-2})	$\log_e$ W yarrow
0	$2.729 - 0.11877t + 0.0030157t^2 - 0.000014843t^3$
194	$-3.412 + 0.17193t - 0.0013123t^2 + 0.000003246t^3$
359	$-3.203 + 0.18132t - 0.0017512t^2 + 0.000006103t^3$
yarrow density (10 cm rhizome fragments m^{-2})	**$\log_e$ W barley**
0	$-12.263 + 0.56566t - 0.0059364t^2 + 0.000021796t^3$
25	$-1.441 + 0.04455t + 0.0017786t^2 - 0.000014397t^3$
50	$-13.115 + 0.61465t - 0.0069851t^2 + 0.000028336t^3$

As all yarrow populations began at the same weight, the increasing reduction in the dry weight with time in the presence of barley must have resulted from a reduction in the relative growth rate (RGR_W). In Figure 4.3 it can be seen that although the presence of barley appeared to initially increase the RGR_W of yarrow, the RGR_W was soon reduced below the rate in the absence of barley, and declined throughout the experimental period. In the absence of barley, the yarrow population maintained a high RGR_W, which did not fall below its initial level until day 93 (6 February). The RGR_W of yarrow was generally lower at 359 than at 194 barley plants m^{-2} but this difference was not significant (Fig. 4.3).

The RGR_W of barley, initially was markedly (100%) higher than the RGR_W of yarrow, but fell more steeply with time (Fig. 4.3). The high density of yarrow caused a small (non significant) reduction in the RGR_W of barley up until day 70, while the low yarrow density apparently reduced the RGR_W of barley in the early part of the experimental period, and

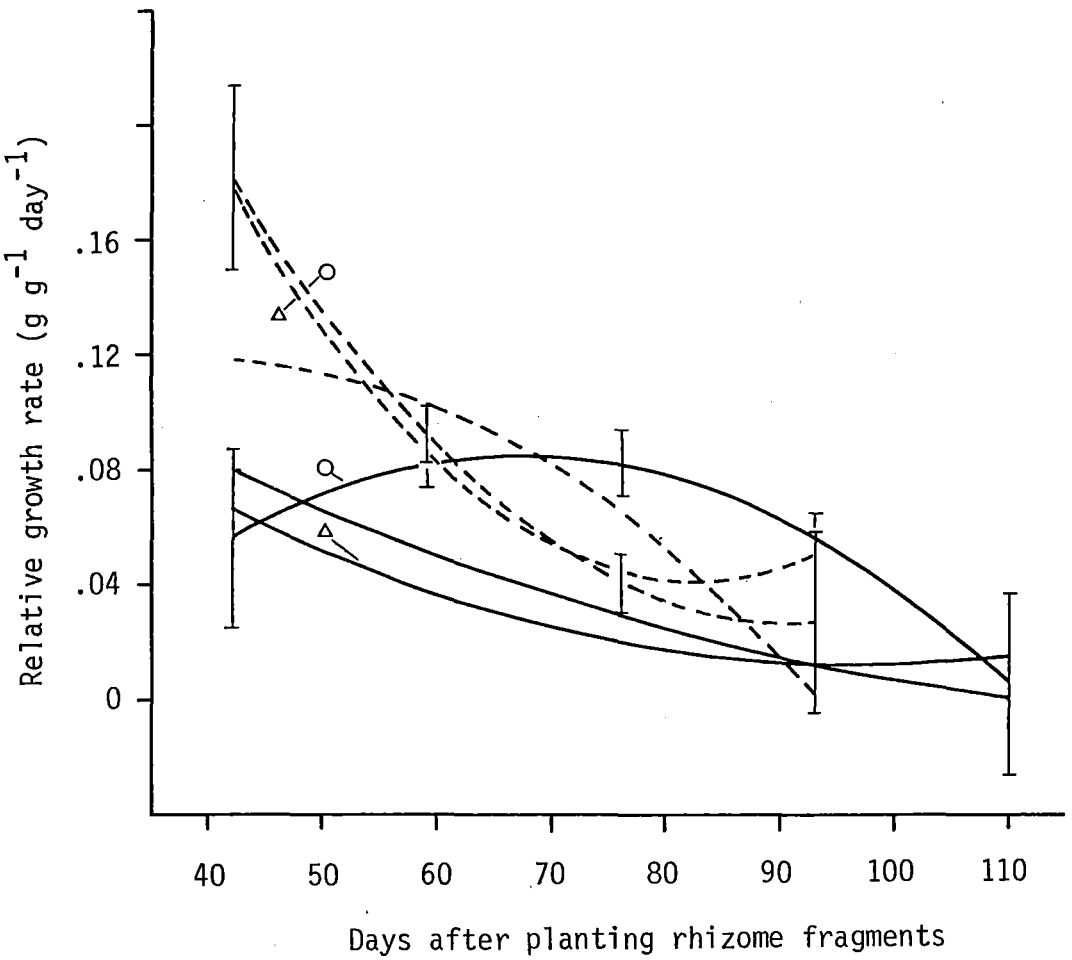


Figure 4.3 Progress curves of relative growth rate derived from Figure 4.2 by differentiation. The bars are the confidence limits for the derived values (95% probability), applying equally to the three curves in each barley and yarrow set. ○---- , ----, △--- , represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively. ○—— , ——, △—— , represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

altered the form of the time-trend.

It is interesting to note that despite their very different RGR_W time-drifts, the yarrow and barley populations growing alone attained similar final total dry weights (Fig. 4.2). The barley reached this by a short burst of very efficient early growth whereas the yarrow population did so by maintaining a more steady rate of moderate efficiency.

4.3.2.2 - Leaf area The changes with time in the logarithms of the leaf area of the yarrow populations were described by cubic polynomials whilst for the barley, quadratics proved to be adequate (Table 4.4). The observed means are given in Appendices V and VIII. The leaf area of the yarrow populations increased with time, reached a maximum at about day 100, and then showed a tendency to decline (Fig. 4.4). By day 59 the leaf areas of yarrow in the presence of 194 barley plants m^{-2} diverged significantly from the areas in the absence of barley, and at 359 plants m^{-2}, there was a further significant reduction. The relative growth rate of leaf area (RGR_A) of yarrow (derived from the equations in Table 4.4) in the absence of barley was maintained at a relatively constant level until day 76 (beginning of flowering), but then declined rapidly with time, becoming negative by day 102, as a net loss in leaf area began to occur owing to senescence (Fig. 4.5). In contrast, the RGR_A of yarrow in the presence of barley, declined with time from the beginning of the experimental period, and was significantly reduced in comparison with the RGR_A without barley, indicating that the efficiency of leaf expansion was greatly impaired in the yarrow population growing with the barley. The RGR_A in the presence of barley also became negative from day 95, indicating leaf senescence.

The leaf area of the barley populations increased with time and reached a maximum earlier than yarrow, at day 70, at the late stem extension, early boot stage, from which time a marked decline owing to leaf senescence occurred (Fig. 4.4). At both densities of yarrow the leaf area of barley was consistently lower than when yarrow was absent, and this reduction was signifiant during the middle phase of growth. However, there was no significant difference between the effects of the low and high densities of yarrow (Fig. 4.4). The RGR_A of barley declined linearly with time and was slightly reduced (non-significantly) during the early phase of association with yarrow at both densities (Fig. 4.5). The RGR_A of barley was negative from day 70 during the period of leaf senescence.

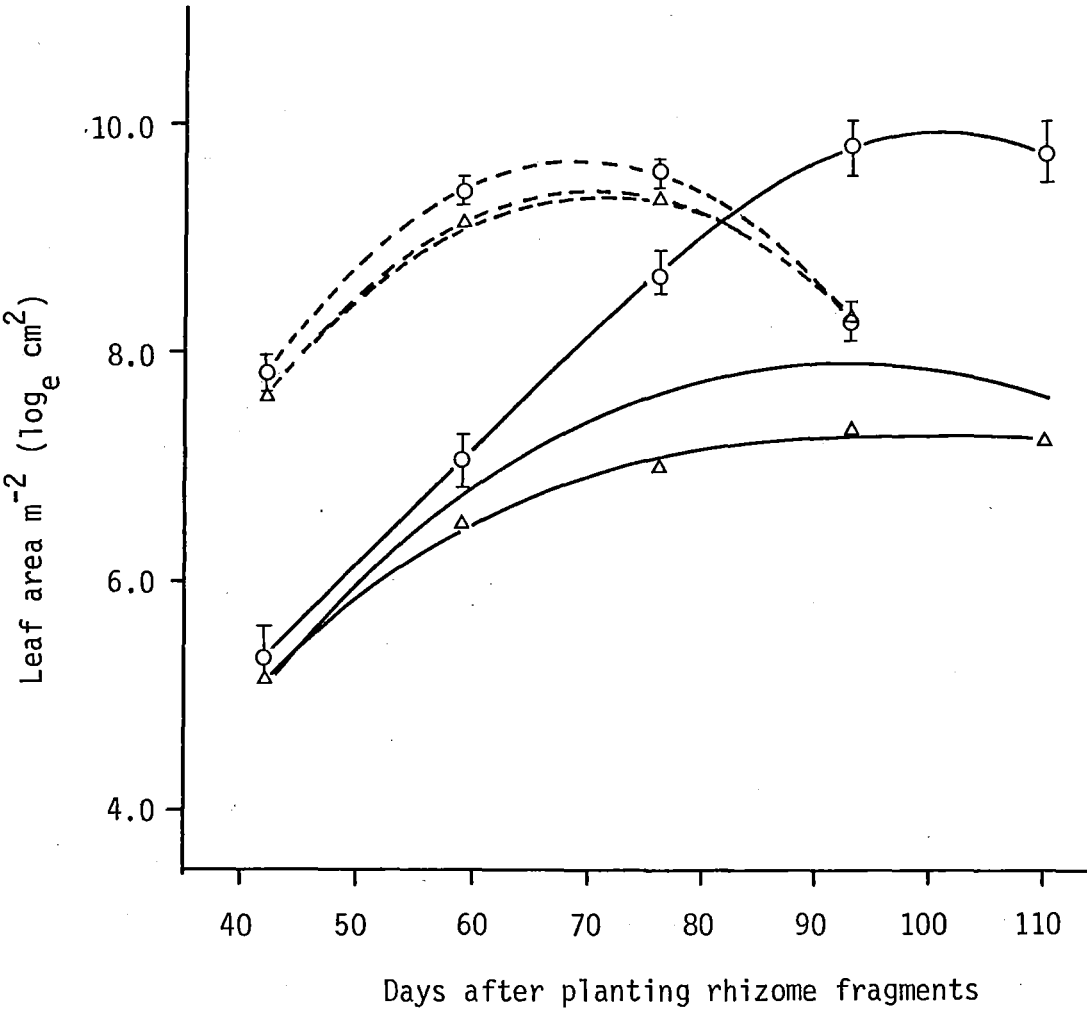


Figure 4.4 Progress curves of total leaf area m^{-2}. The points are the observed means of the logarithms for both densities of the species; means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves in each barley and yarrow set. o--- o, --- , Δ---Δ, represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively. o—— o, —— , Δ—— Δ, represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

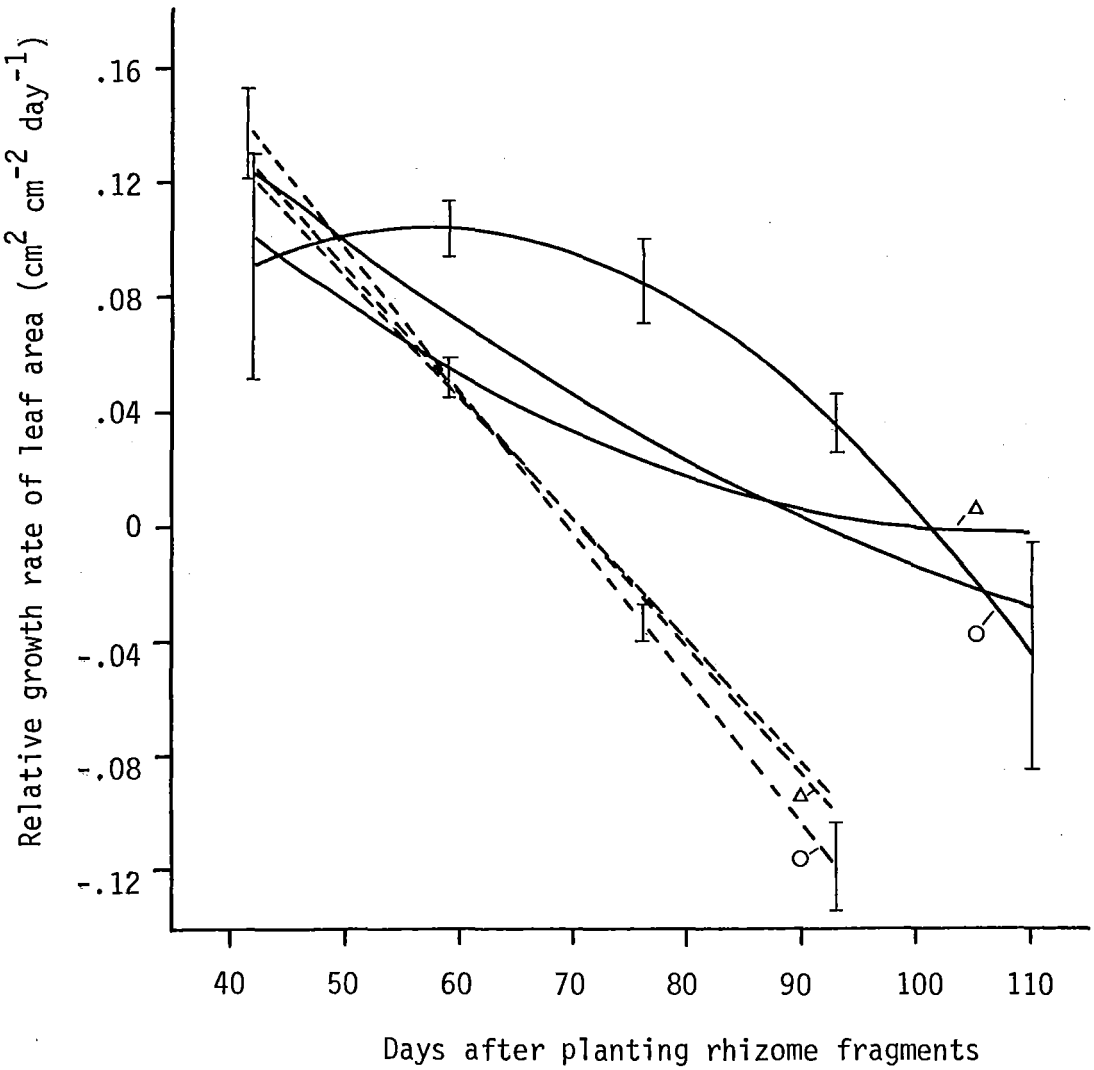


Figure 4.5 Progress curves of relative growth rate of leaf area derived from Figure 4.4 by differentiation. The bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves in each barley and yarrow set. o——, ——, Δ——, represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively. o---, ---, Δ---, represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively.

Table 4.4 Regression equations for $\log_e$ leaf area m^{-2} (A). t in days from planting rhizome fragments; A in cm^2

barley density (plants m^{-2})	$\log_e$ A yarrow
0	$4.412 - 0.078307t + 0.0031587t^2 - 0.000018225t^3$
194	$-3.297 + 0.28228t - 0.0021680t^2 + 0.000004600t^3$
359	$-2.535 + 0.27672t - 0.0025766t^2 + 0.000007919t^3$
yarrow density (10 cm rhizome fragments m^{-2})	**$\log_e$ A barley**
0	$-2.364 + 0.34746t - 0.0025057t^2$
25	$-1.211 + 0.29858t - 0.0021079t^2$
50	$-1.566 + 0.31137t - 0.0022074t^2$

4.3.2.3 Leaf dry weight To allow a full growth analysis of the data, the growth curves of leaf dry weight were also calculated. The observed means are given in Appendices V and VIII. Cubic polynomials adequately described the time-changes in the logarithms for the yarrow and barley populations (Table 4.5). Leaf dry weight of yarrow increased with time, reaching a plateau at day 80 in the presence of barley, but continued to increase until day 110 without barley (Fig. 4.6). From day 60, the yarrow leaf weights at 194 barley plants m^{-2} were significantly lower than in the absence of barley and a further significant reduction occurred with 359 m^{-2}.

The leaf dry weight of barley followed a similar pattern to leaf area, increasing to a maximum between 65 and 70 and then declining as the leaves senesced (Fig. 4.6). The leaf weight of the barley was consistently lower in the presence of yarrow, reaching significance near day 60 at 194 barley plants m^{-2}.

4.3.2.4 Net assimilation rate The net assimilation rate (NAR) of yarrow declined with time, but did so more rapidly in the presence of barley, so that by day 59, the NAR of yarrow in the presence of barley

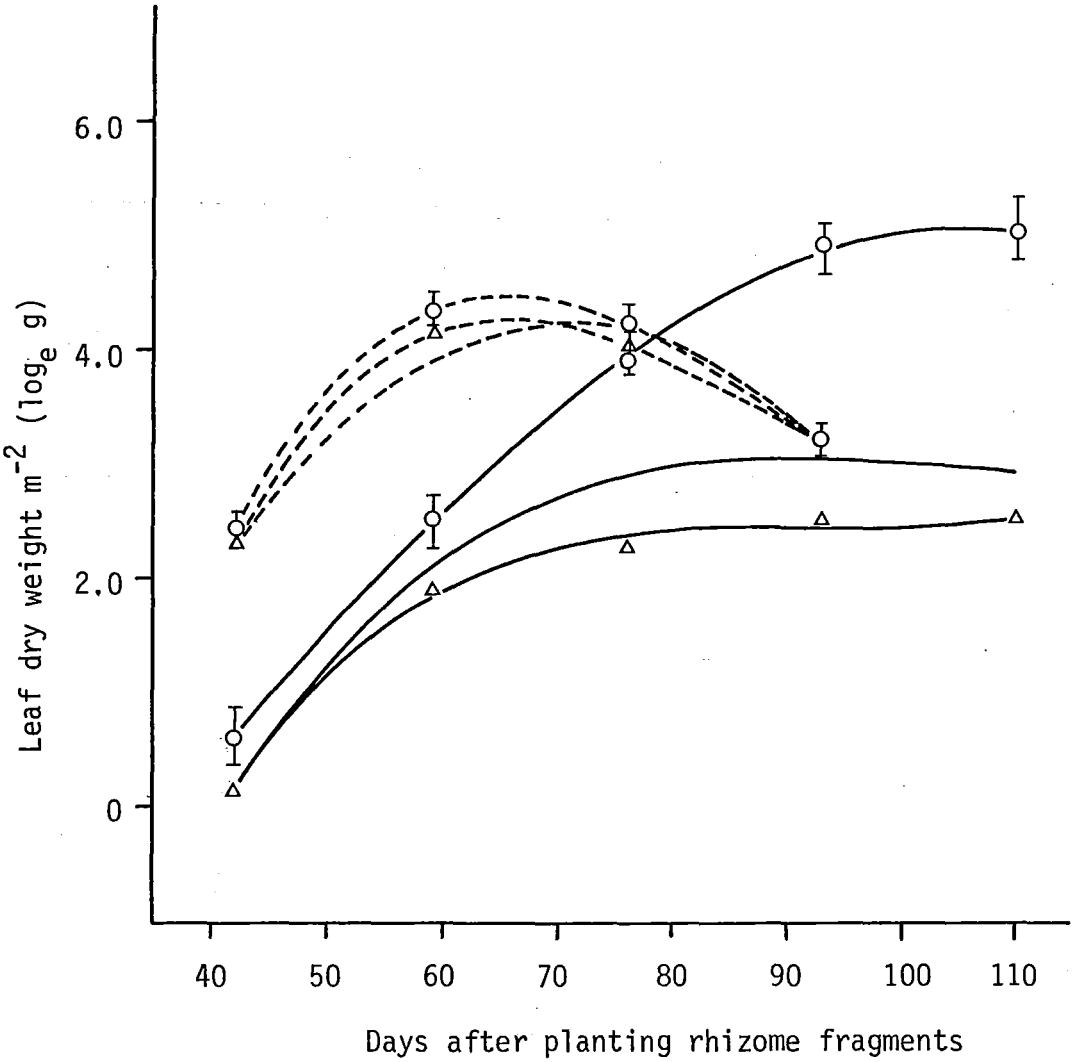


Figure 4.6 Progress curves of leaf weight m^{-2}. The points are the observed means of the logarithms for both densities of the species; means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves in each barley and yarrow set. o---o, --- ,Δ---Δ, represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively. o——o, —— ,Δ——Δ, represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

was significantly lower than without barley (Fig. 4.7 a). There was no significant difference in the NAR of yarrow at 359 compared to 194 barley plants m^{-2}. The NAR of yarrow in the presence of barley appeared to be higher initially than without barley but the large size of the confidence limits shows the difference was not significant.

Table 4.5 Regression equations for $\log_e$ leaf dry weight m^{-2} (LW). t in days from planting rhizome fragments; LW in g.

barley density (plants m^{-2})	$\log_e$ LW yarrow
0	$-4.670 + 0.12353t + 0.0002901t^2 - 0.000005540t^3$
194	$-12.568 + 0.47482t - 0.0047490t^2 + 0.000015568t^3$
359	$-12.054 + 0.47910t - 0.0052691t^2 + 0.000019277t^3$
yarrow density (10 cm rhizome fragments m^{-2})	**$\log_e$ LW barley**
0	$-17.750 + 0.83318t - 0.0099201t^2 + 0.000036383t^3$
25	$-8.104 + 0.36752t - 0.0030273t^2 + 0.000004135t^3$
50	$-18.453 + 0.87076t - 0.010721t^2 + 0.000041543t^3$

In contrast, the NAR of the barley population without and with the high density of yarrow, remained constant until day 76 (early boot stage) after which it increased sharply with time (Fig. 4.7 b). At the low density of yarrow, an anomoly was apparent, as the NAR increased until day 85 and then fell sharply. The presence of the high density of yarrow did not alter the NAR of barley, but at the low density, NAR was increased at day 76.

4.3.2.5 Leaf area ratio; specific leaf area; leaf weight ratio

The leaf area ratios (LAR) of the yarrow and barley populations are presented in Figure 4.8 from which two important elements may be discerned. Neither species significantly altered the LAR of the other species. Secondly, it can be seen that the barley had initially, a considerably

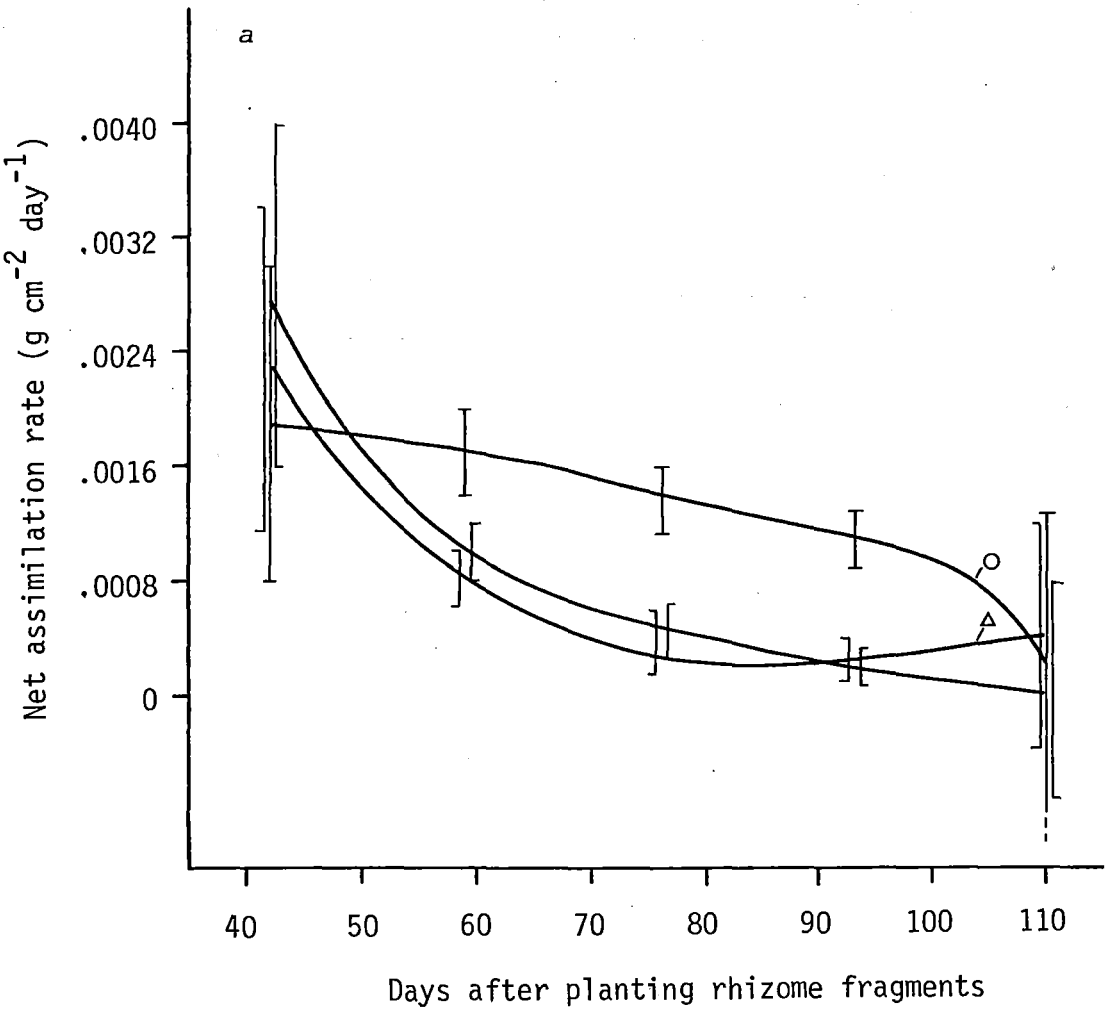


Figure 4.7 See page 121.

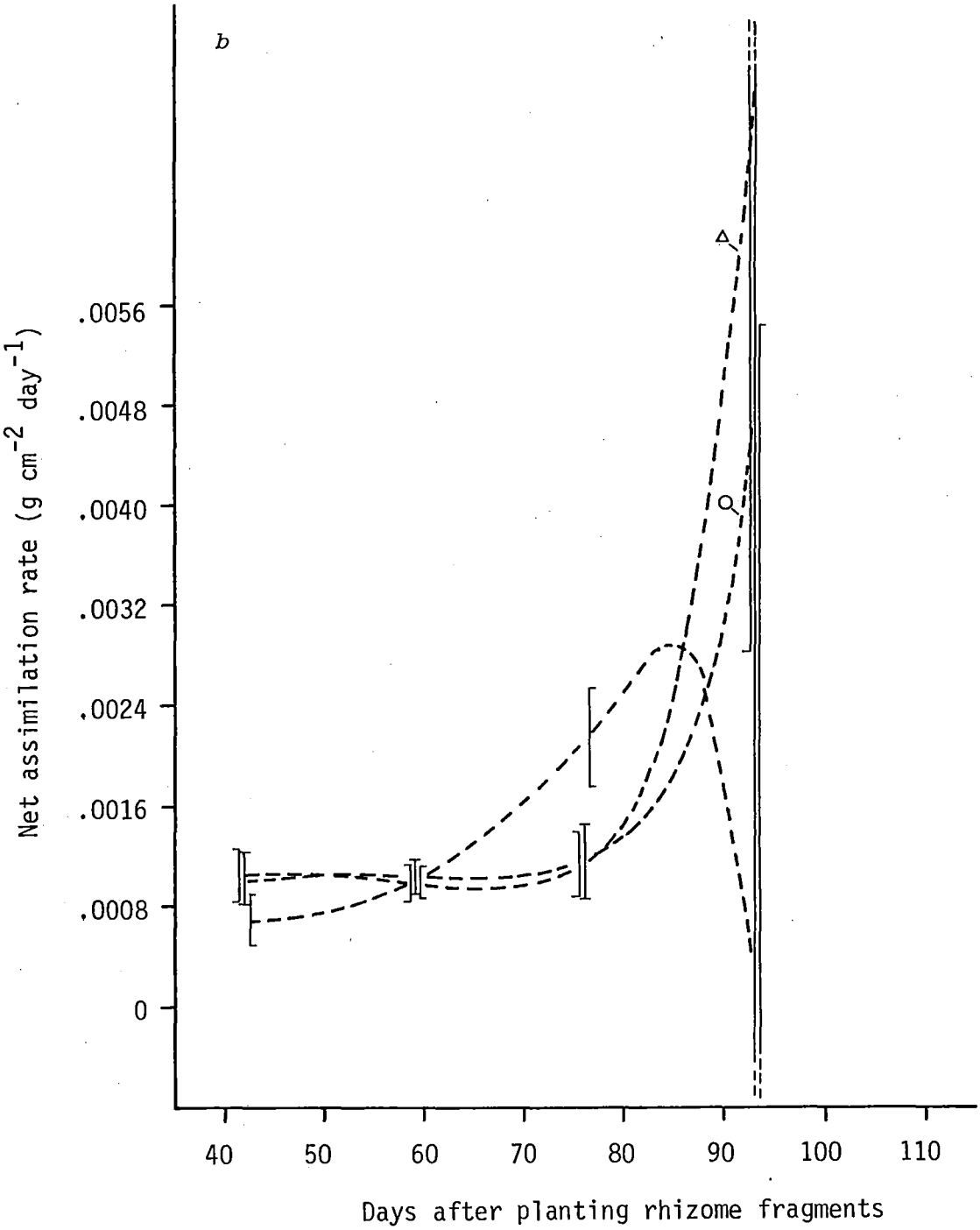


Figure 4.7 Progress curves of net assimilation rate, derived from fitted curves of $\log_e W$ and $\log_e A$ by differentiation and division. Bars are the confidence limits for derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. *b*. o– – – –, – – – –, Δ– – – –, represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively. *a*. o——, ——, Δ——, represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

higher LAR, i.e. was more leafy, than was the yarrow, but the LAR of barley fell steeply with time, reaching almost zero by day 93 owing to leaf senescence. In contrast, the LAR of yarrow increased with time until day 80 and then declined gently during the flowering stage.

The specific leaf area (SLA) of yarrow was significantly increased between day 42 and 59 in the presence of barley at both densities, but during the remainder of the experimental period, SLA of yarrow was not affected (Fig. 4.9). There were however, no significant affects of yarrow on the SLA of barley. It can also be seen in Figure 4.9, that the SLA was higher in the barley populations than in the yarrow.

The leaf weight ratio (LWR) curves (Fig. 4.10) followed similar trends to those of LAR (Fig. 4.8) and were similarly unaffected by the presence of the other species. The barley populations initially had a higher LWR than the yarrow populations, but this declined rapidly throughout the experiment, whereas the LWR of the yarrow initially increased to a maximum at about day 70, and then declined (Fig. 4.10).

4.3.2.6 Rhizomes Rhizomes were initiated by all individual yarrow plants in the period between the first and second harvests (day 42 to day 59), when in the late rosette, early stem extension phase of growth. The rhizomes were markedly retarded in growth in the presence of barley and by the time of the final harvest (day 110), at 194 and 359 barley plants m^{-2}, their dry weight was only 4 and 2% respectively of the amount in the absence of barley (Fig. 4.11).

The changes with time in the logarithms of rhizome dry weight from day 59 were described by quadratic regressions; the observed means are given in Appendix V. The equations are given in Table 4.6 and the growth curves presented in Figure 4.12 from which it can be seen that in the presence of barley at 194 plants m^{-2}, rhizome dry weight was significantly reduced, and was further reduced at 359 plants m^{-2}. The relative growth rate of rhizome dry weight (RGR_R) was generally reduced in the presence of barley, but this only reached significance between day 42 and 76 with 359 barley plants m^{-2}, and at day 76 with 194 plants m^{-2} (Fig. 4.13). These reductions in the accumulation of dry matter in rhizome tissue in the presence of barley were associated with marked reductions in rhizome initiation as indicated by the reduced number of

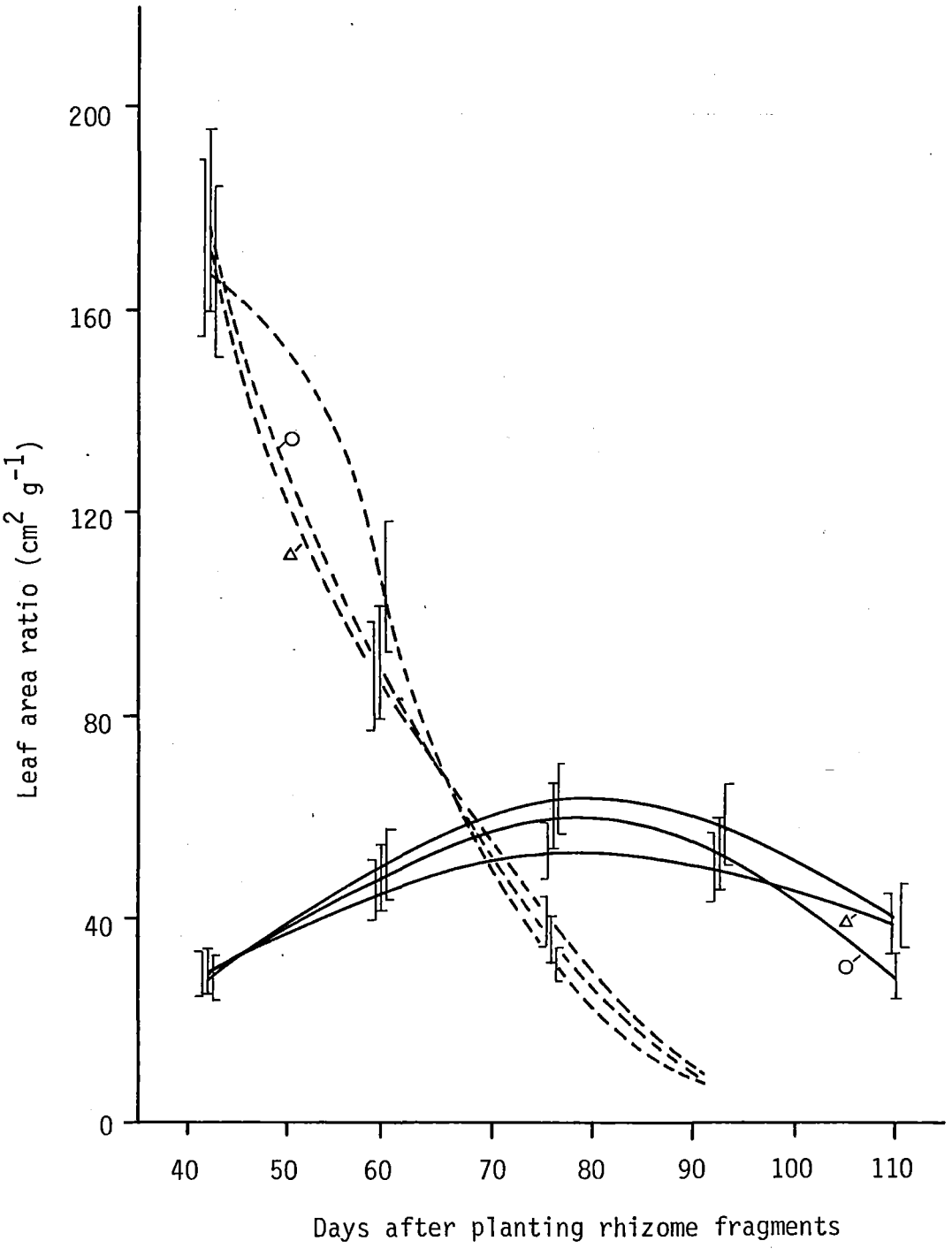


Figure 4.8 Progress curves of leaf area ratio derived from fitted curves of $\log_e A$ and $\log_e W$ by subtraction. Bars are the confidence limits for the derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. o---- , ----, Δ---- , represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively. o—— , ——, Δ—— , represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

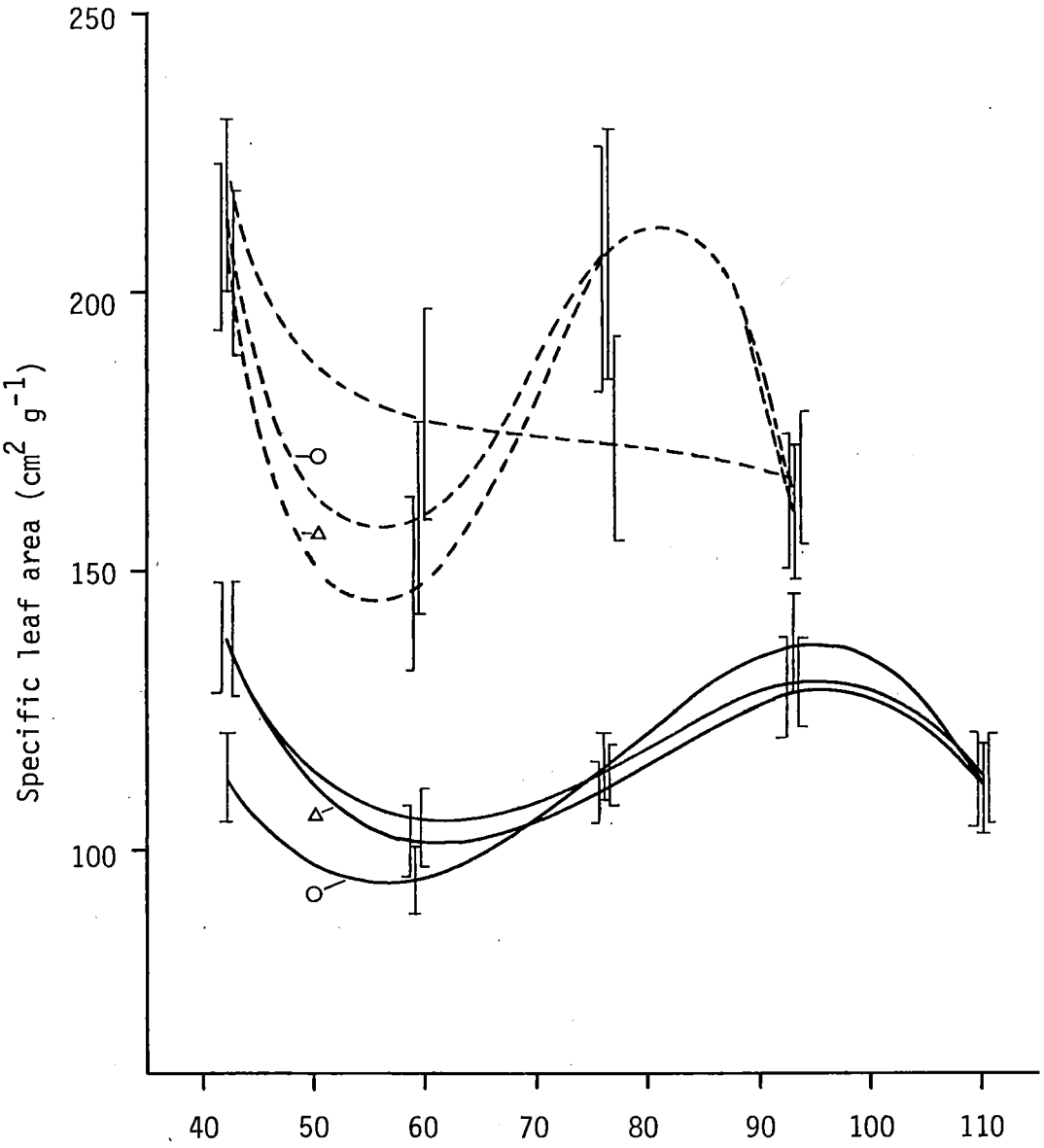


Figure 4.9 Progress curves of specific leaf area derived from fitted curves of $\log_e A$ and $\log_e W$ by subtraction. Bars are the confidence limits for the derived values (95% probability) and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species.

o--- , ---, Δ--- , represent barley at yarrow densities of 0, 25 and 50, 10 cm rhizome fragments m^{-2} respectively. o—— , ——, Δ—— , represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

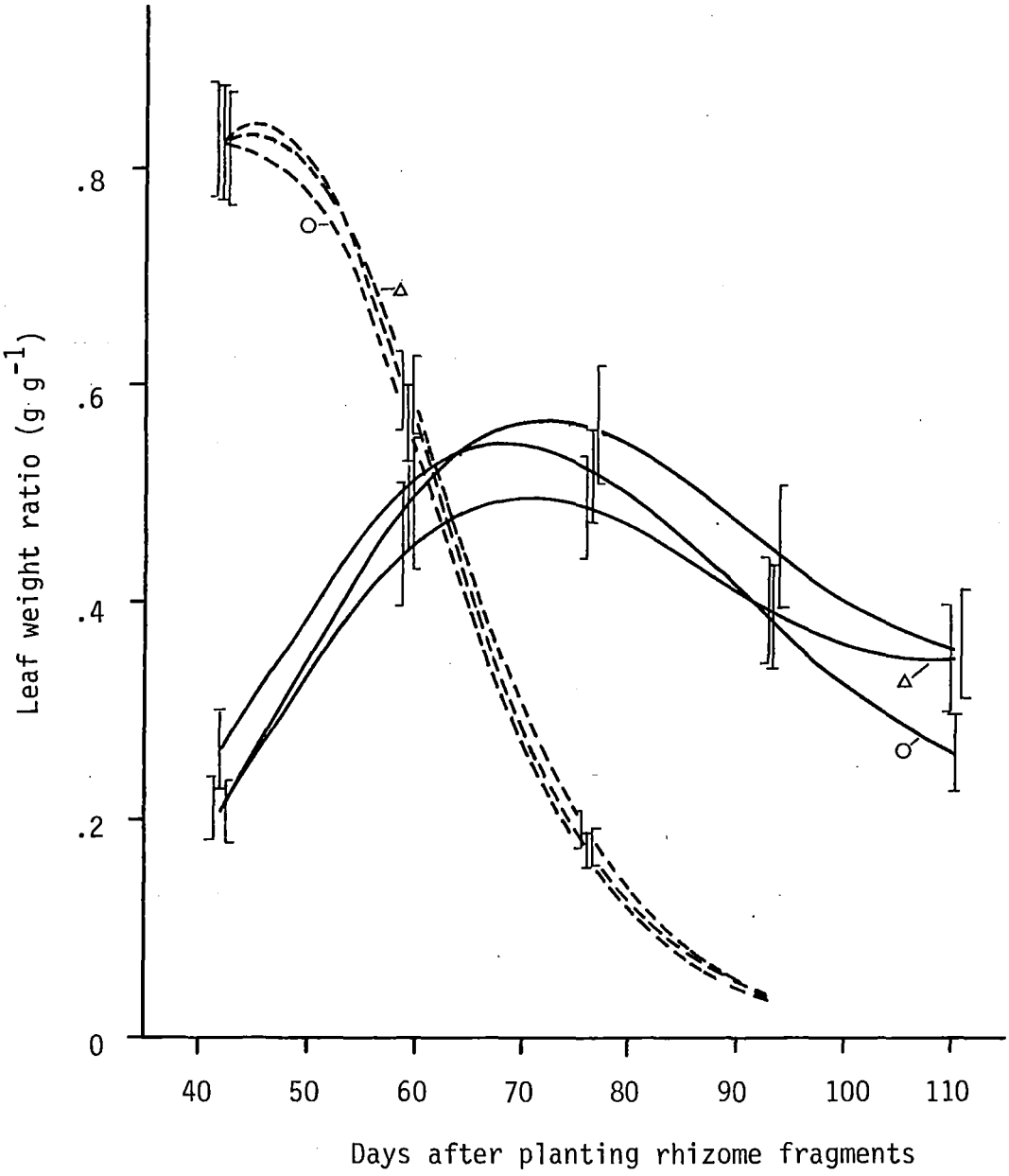


Figure 4.10 Progress curves of leaf weight ratio derived from fitted curves of $\log_e W$ and $\log_e LW$ by subtraction. Bars are the confidence limits for the derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species.

o---, ---, Δ---, represent barley at yarrow densities of 0, 25 and 50 10 cm rhizome fragments m^{-2} respectively. o——, ——, Δ——, represent yarrow at barley densities of 0, 194 and 359 plants m^{-2} respectively.

rhizomes formed (Fig. 4.14) and a striking reduction in the total length of rhizomes (Fig. 4.15). Thus the reduction in dry weight of the rhizome system in the presence of barley was due both to diminished initiation, as well as reduced RGR_R of the rhizomes produced. The means from which Figures 4.14 and 4.15 were constructed are presented in Appendices XV and XIV respectively.

Table 4.6 Regression equations for $\log_e$ new yarrow rhizome dry weight m^{-2} (R), and $\log_e$ total dry weight m^{-2} (W), from t = 59 (harvest 2) to t = 110 (harvest 5). t in days from planting rhizome fragments; R and W in g.

barley density (plants m^{-2})	
	$\log_e R$
0	$-12.493 + 0.28058t - 0.0011617t^2$
194	$-8.959 + 0.18689t - 0.0008734t^2$
359	$-3.843 + 0.04308t - 0.0000619t^2$
	$\log_e W$
0	$-5.487 + 0.19090t - 0.00075173t^2$
194	$-1.478 + 0.10104t - 0.00047076t^2$
359	$0.302 + 0.051208t - 0.00019317t^2$

The ratio of rhizome dry weight : total plant dry weight (rhizome weight ratio (RWR)) is presented in Figure 4.16. To simplify the calculation of this ratio, it was necessary to fit a curve to the logarithms of total plant dry weight ($\log_e W$) from day 59 to day 110. The equations of these curves are given in Table 4.6 and it will be noticed that they differ from the growth curves of $\log_e W$ previously fitted to the data from day 42 to 110 (Table 4.3); the former including terms only up to the quadratic. In Figure 4.16, it can be seen that the RWR increased with time in the absence and presence of barley, but was significantly reduced in the presence of 194 barley plants m^{-2}, and reduced further with 359 plants m^{-2}. It would appear that the allocation of dry matter to rhizome growth was very susceptible to interference from the barley, in contrast to the relative constancy of the allocation to leaf tissue (Fig. 4.10).

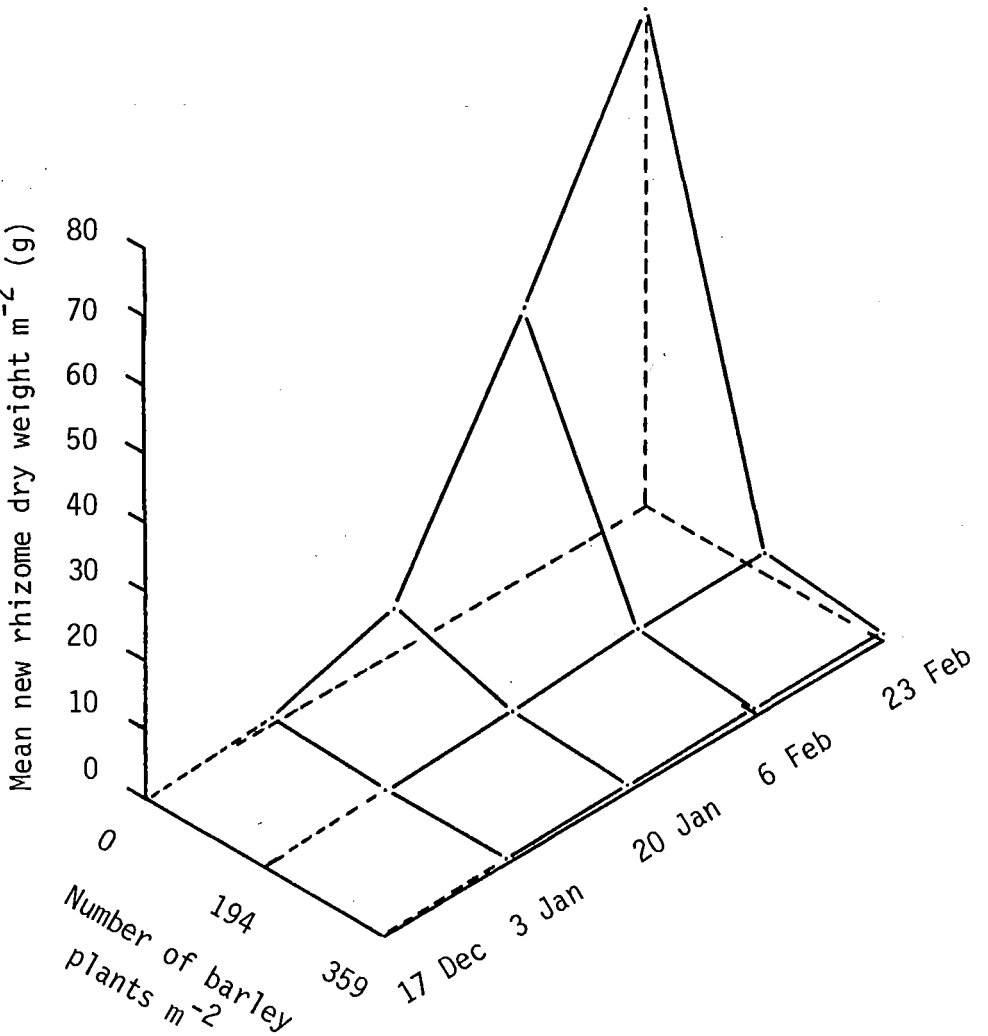


Figure 4.11 New rhizome dry weight m^{-2} as related to time and barley density. Points are the back-transformed observed means of the logarithms for both yarrow densities.

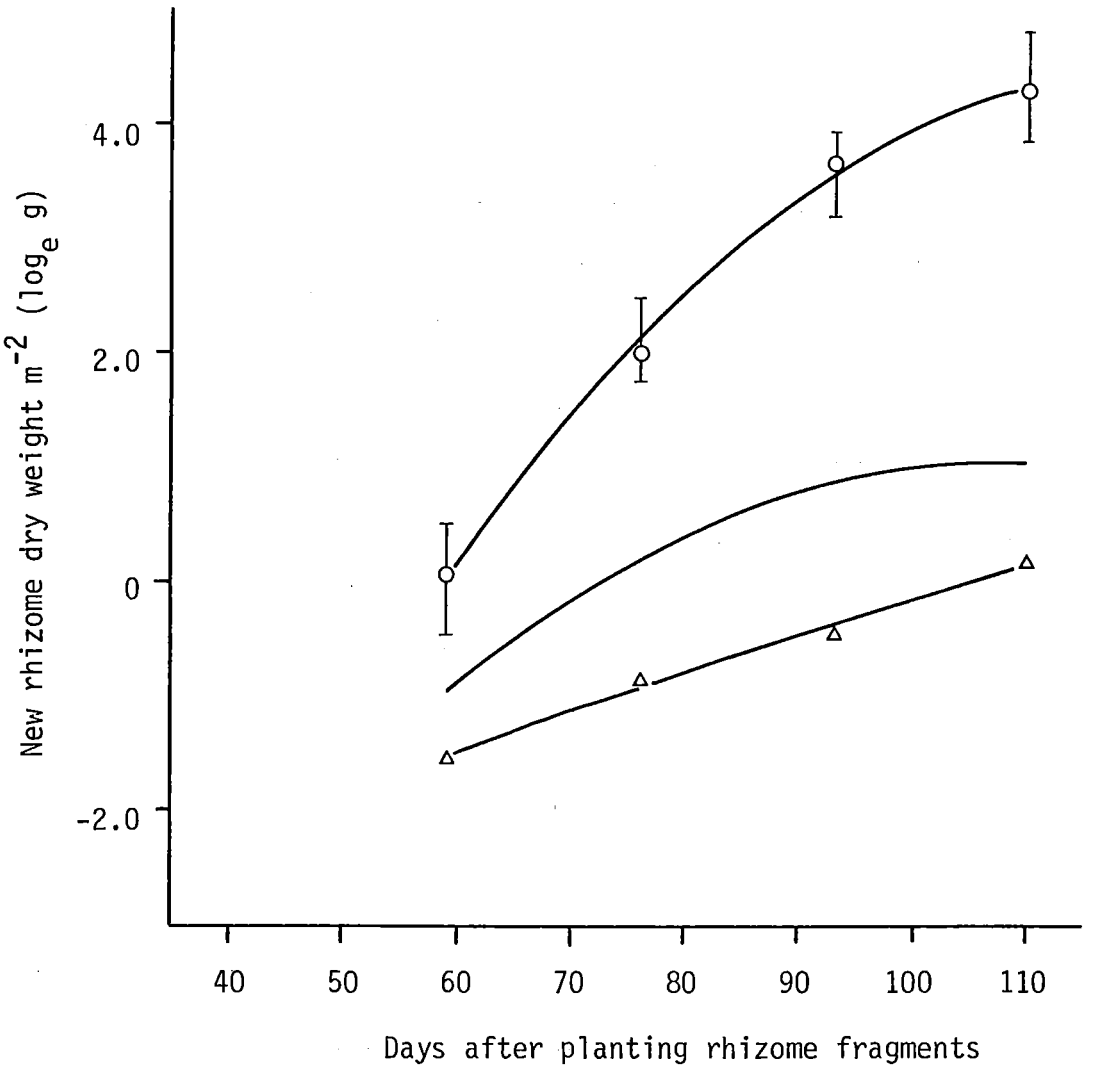


Figure 4.12 Progress curves of new rhizome dry weight m^{-2}. The points are the observed means of the logarithms for both yarrow densities; the means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves. o——o, ——, Δ——Δ, represent barley densities of 0, 194 and 359 plants m^{-2} respectively.

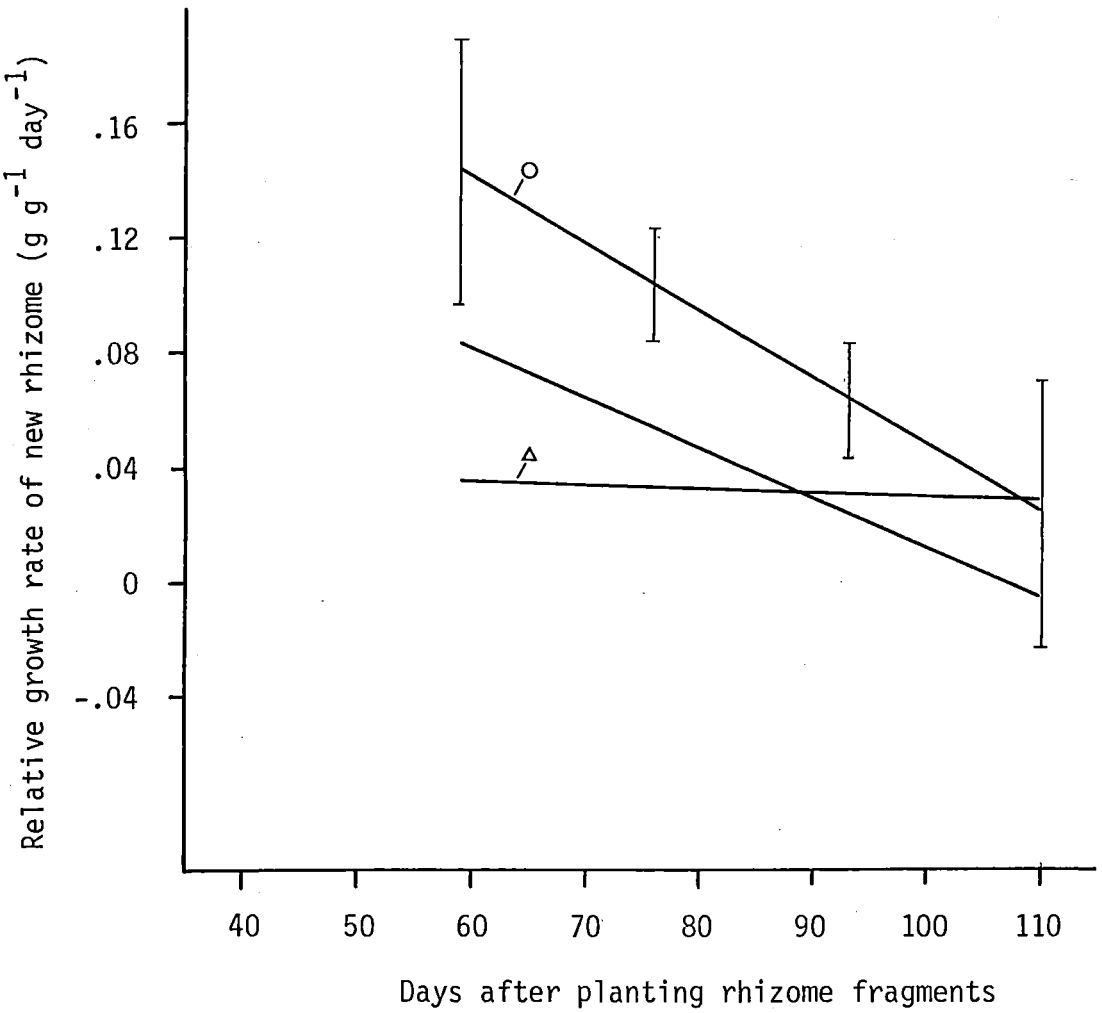


Figure 4.13 Progress curves of rhizome relative growth rate, derived from Figure 4.12 by differentiation. The bars are the confidence limits for the derived values (95% probability), applying equally to the three curves. o——o, ——, Δ——Δ, represent barley densities of 0, 194 and 359 plants m^{-2} respectively.

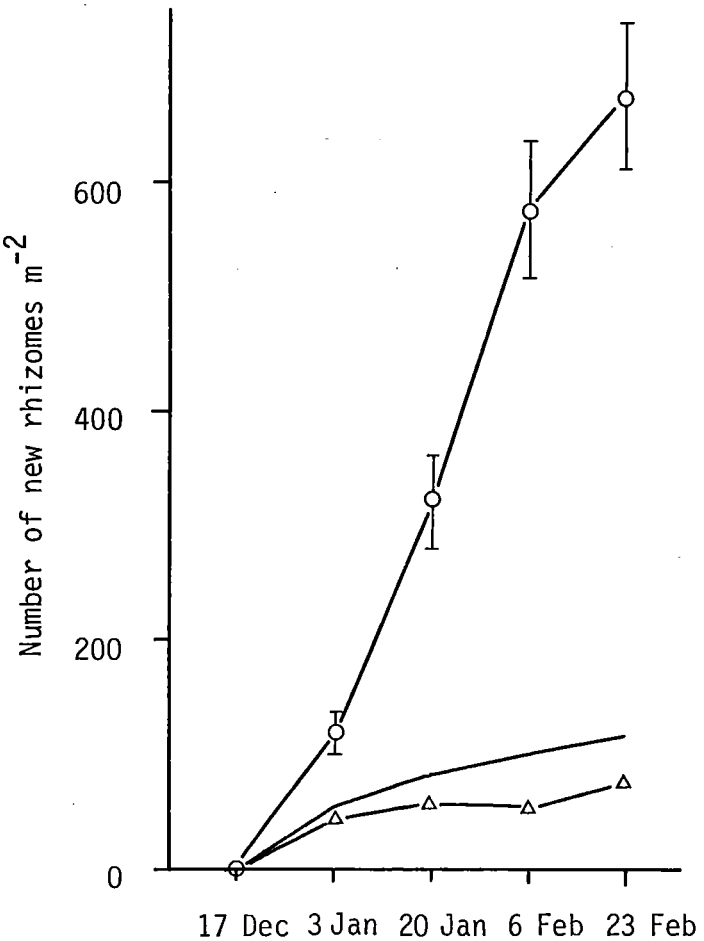


Figure 4.14 Rhizome number m^{-2} as related to time and barley density. The points are the observed means for both yarrow densities; means of 12 samples, and the bars are the confidence limits for these means (95% probability). o—— o, ——, △—— △, represent barley densities of 0, 194 and 359 plants m^{-2} respectively.

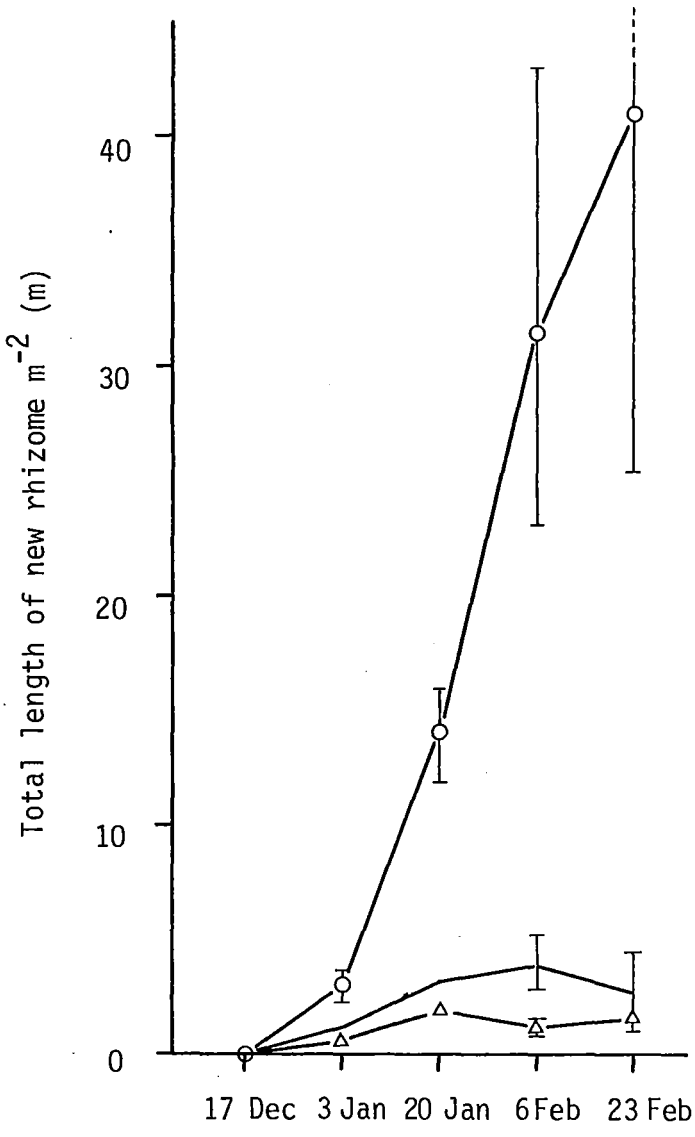


Figure 4.15 Rhizome length m^{-2} as related to time and barley density. The points are the observed means for both yarrow densities; means of 12 samples, and the bars are the confidence limits for the means (95% probability) o——o, ——, Δ——Δ, represent barley densities of 0, 194 and 359 plants m^{-2} respectively.

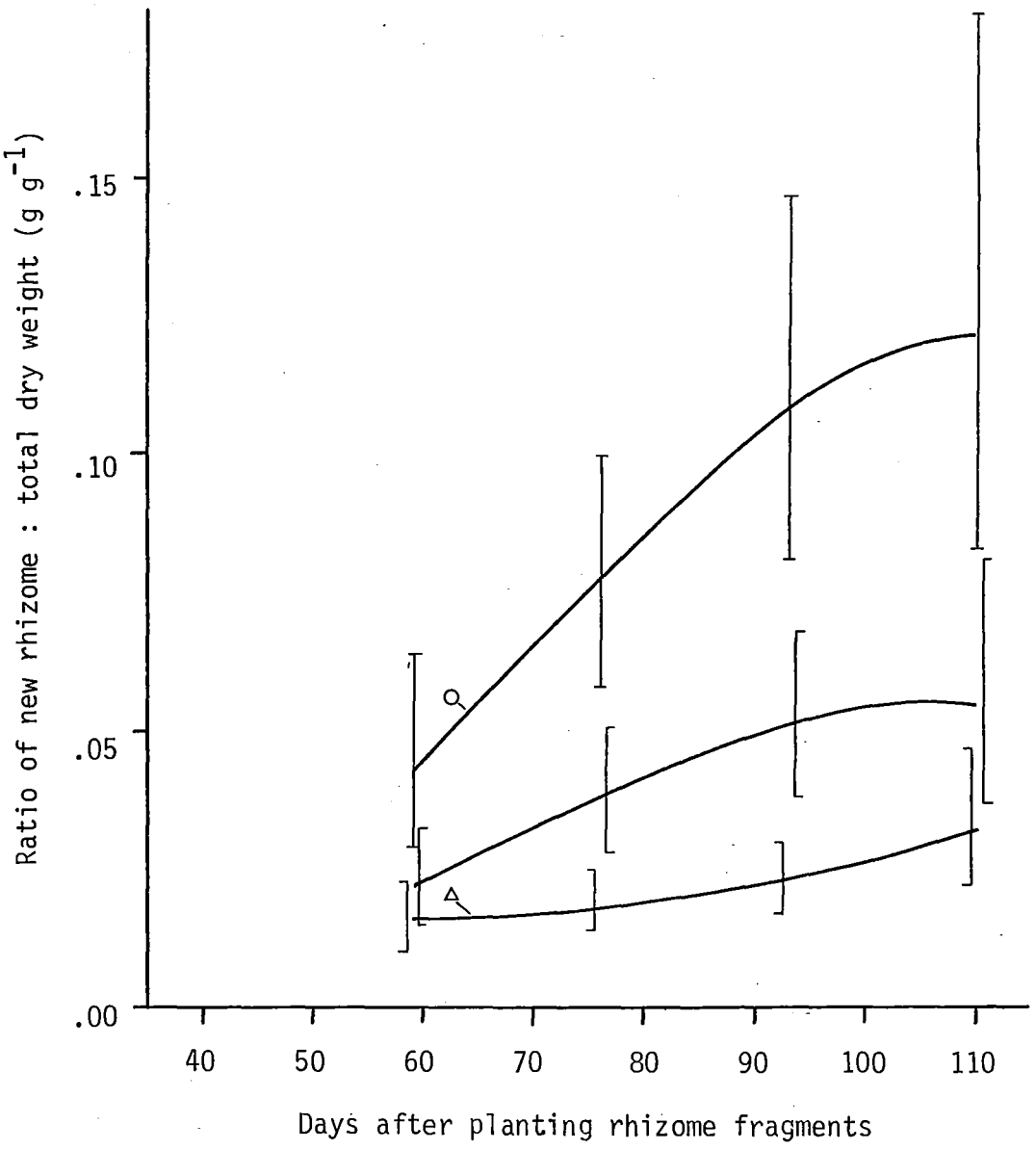


Figure 4.16 Progress curves of new rhizome dry weight : total dry weight ratio derived from fitted curves of $\log_e R$ and $\log_e W^a$ by subtraction. Bars are the confidence limits for the derived values (95% probability) and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. o—— , ——, Δ—— , represent barley densities of 0, 194 and 359 plants m^{-2} respectively.
a, logarithms of W from day 59 to day 110; see Table 4.6.

4.3.2.7 Yarrow flower stems After emergence of the vertical subterranean shoots early in December, the young yarrow plants remained in the rosette form for approximately five weeks. It was not until harvest 2 (day 59) that stem elongation was recorded and it was apparent that fewer of the stems were elongating in the presence of barley than in its absence. The histograms in Figure 4.17 show the frequencies of shoots in height classes of 40 mm (measured from point of attachment of the shoot to the planted rhizome fragment), and were derived from the raw data on individual shoot heights over the six replicates, and averaged over both yarrow densities. The means on which these histograms are based are given in Appendix XVI. The trend of reduced numbers of elongating flower stems continued throughout the experimental period, until at the time of the final harvest (day 110), only 14% of the primary shoots remained as rosettes (less than 80 mm in height), in the absence of barley. In the presence of barley at 194 and 359 plants m^{-2}, 71% and 76% of the shoots respectively remained as rosettes. Although the distribution of shoot heights was markedly altered by barley, possibly due to suppression of flower initiation, many of the shoots which did elongate reached heights of equal stature to those in the population without barley (Fig. 4.17), and of equal or greater stature than the barley plants (compare Fig. 4.17 with Fig. 4.21).

The increases in the logarithms of stem dry weight (see Appendix V for observed means) with time were described by cubic regression equations (Table 4.7) and are illustrated in Figure 4.18. Barley at 194 plants m^{-2} substantially reduced the production of stem dry matter in the yarrow population, but the further reduction with 359 plants m^{-2} was not significant. Not only was flower stem dry weight reduced as a consequence of reduced numbers, but it was also evident that stems which were formed in the presence of barley, grew less efficiently as indicated by the reduced relative growth rates (RGR_S) shown in Figure 4.19. It can also be seen from Figure 4.19 that stem growth was maximal on about day 80 (as the first flowers approached anthesis) but thereafter declined rapidly to zero, indicating the end of this phase of growth.

The ratio of stem dry weight : total plant dry weight (stem weight ratio (SWR)) was not affected by the presence of barley until stem elongation began, from which time the SWR was significantly reduced at both

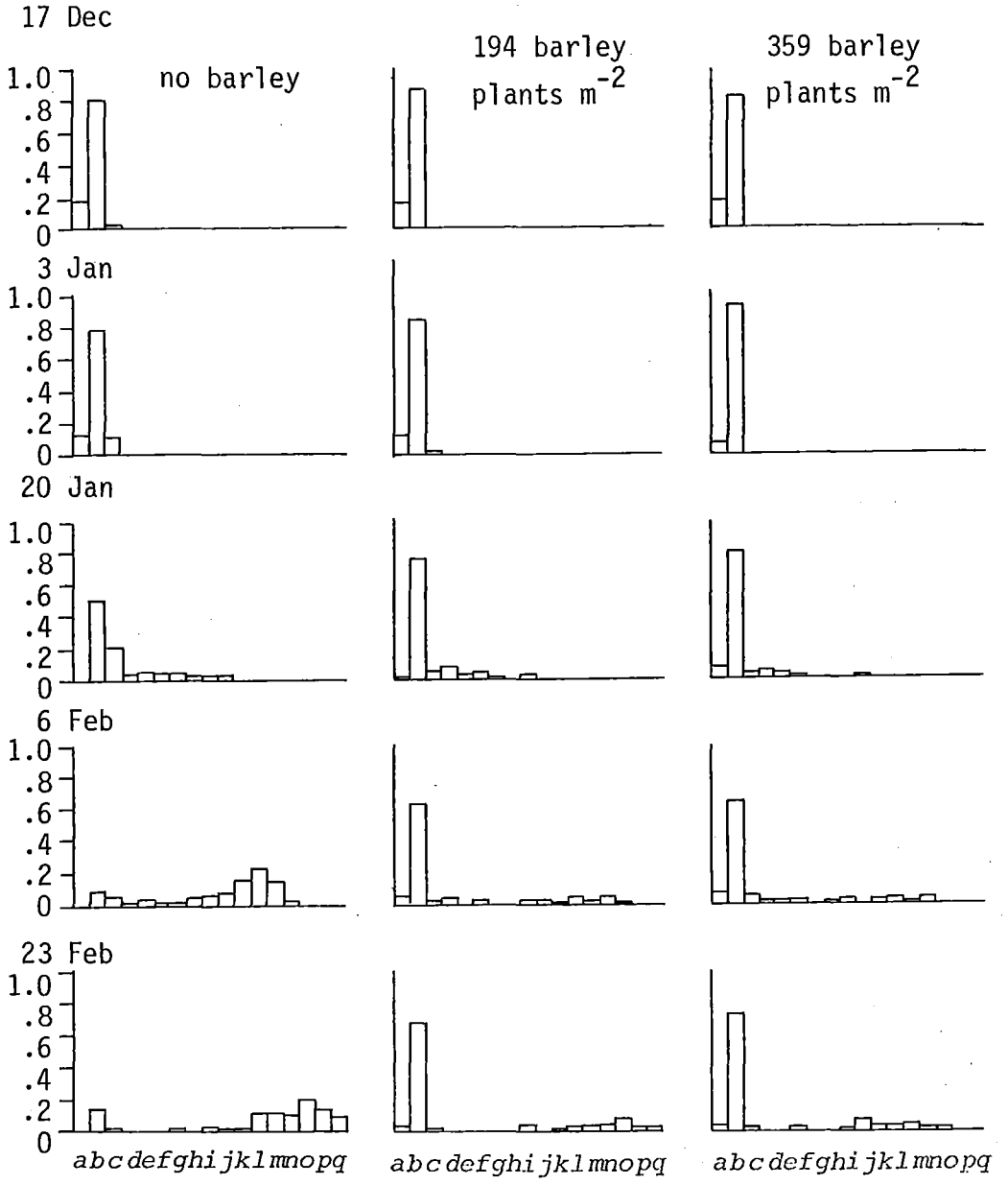


Figure 4.17 The effect of barley on the frequency distribution of yarrow stem height. The distributions are those of all the sampled shoots for both densities of yarrow. Height classes of 40 mm, measured from the point of attachment of the shoot with the planted rhizome fragment. *a*. 1 - 40; *b*. 41 - 80; *c*. 81 - 120; *d*. 121 - 160; *e*. 161 - 200; *f*. 201 - 240; *g*. 241 - 280; *h*. 281 - 320; *i*. 321 - 360; *j*. 361 - 400; *k*. 401 - 440; *l*. 441 - 480; *m*. 481 - 520; *n*. 521 - 560; *o*. 561 - 600; *p*. 601 - 640; *q*. 641 - 680.

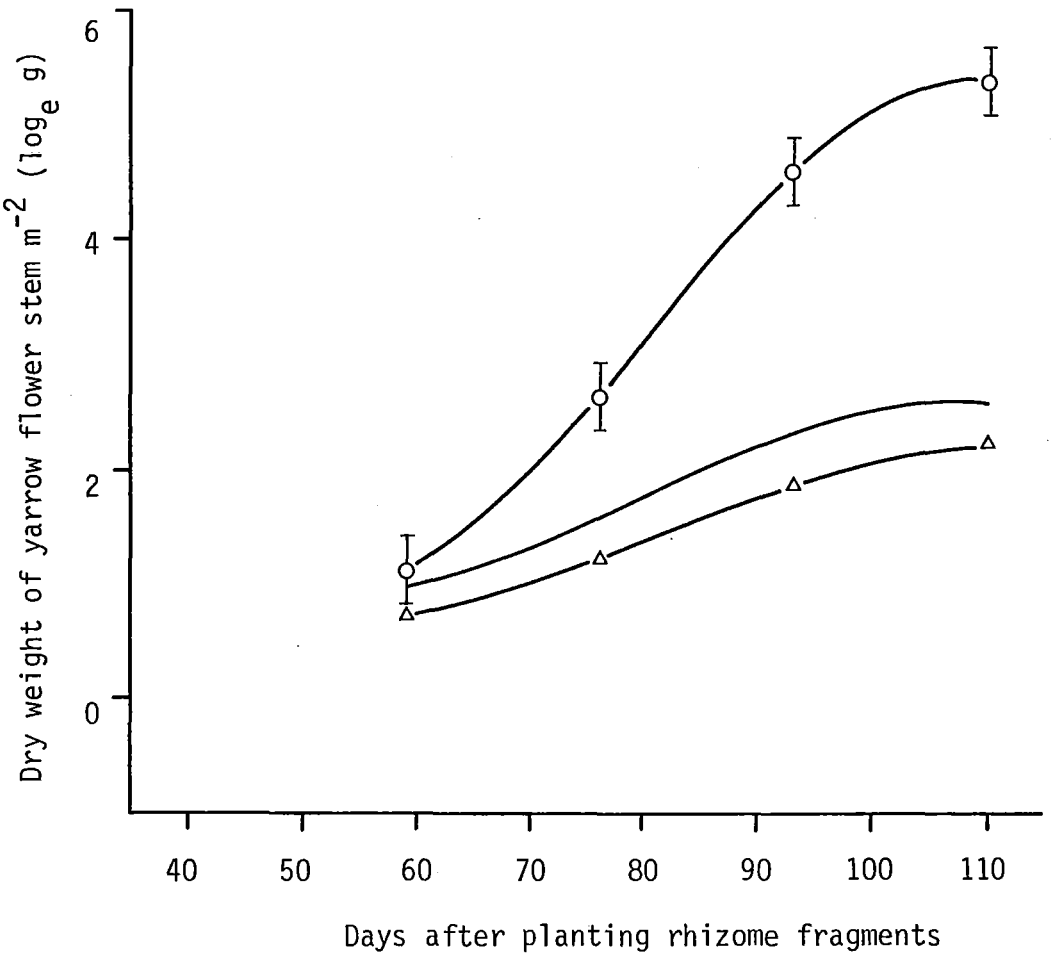


Figure 4.18 Progress curves of yarrow stem dry weight m^{-2}. The points are the observed means of the logarithms for both yarrow densities; the means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves. o——o, ——, Δ——Δ, represent barley densities of 0, 194 and 359 plants m^{-2} respectively.

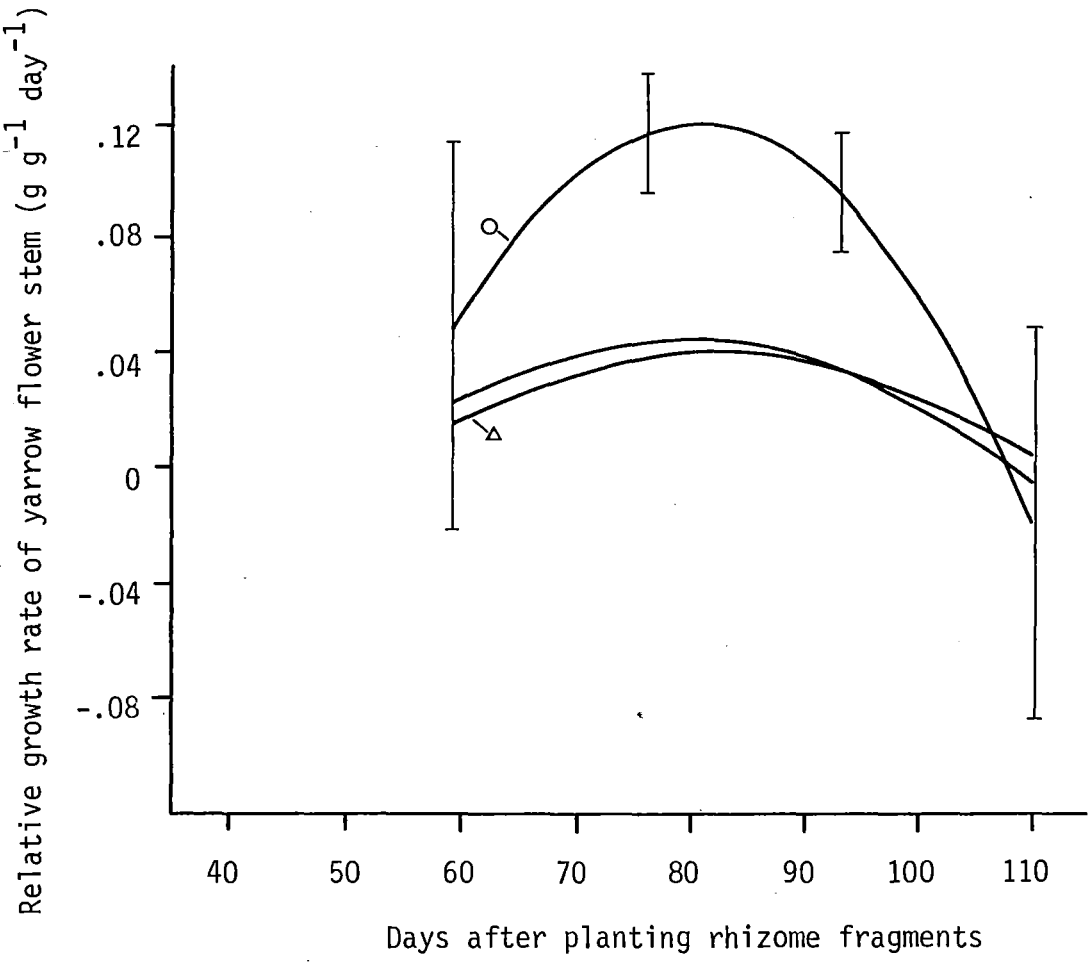


Figure 4.19 Progress curves of relative growth rate of yarrow stem dry weight, derived from Figure 4.18 by differentiation. The bars are the confidence limits for the derived values (95% probability), applying equally to the three curves. ○—— , —— , △—— , represent barley densities of 0, 194 and 359 plants m^{-2} respectively.

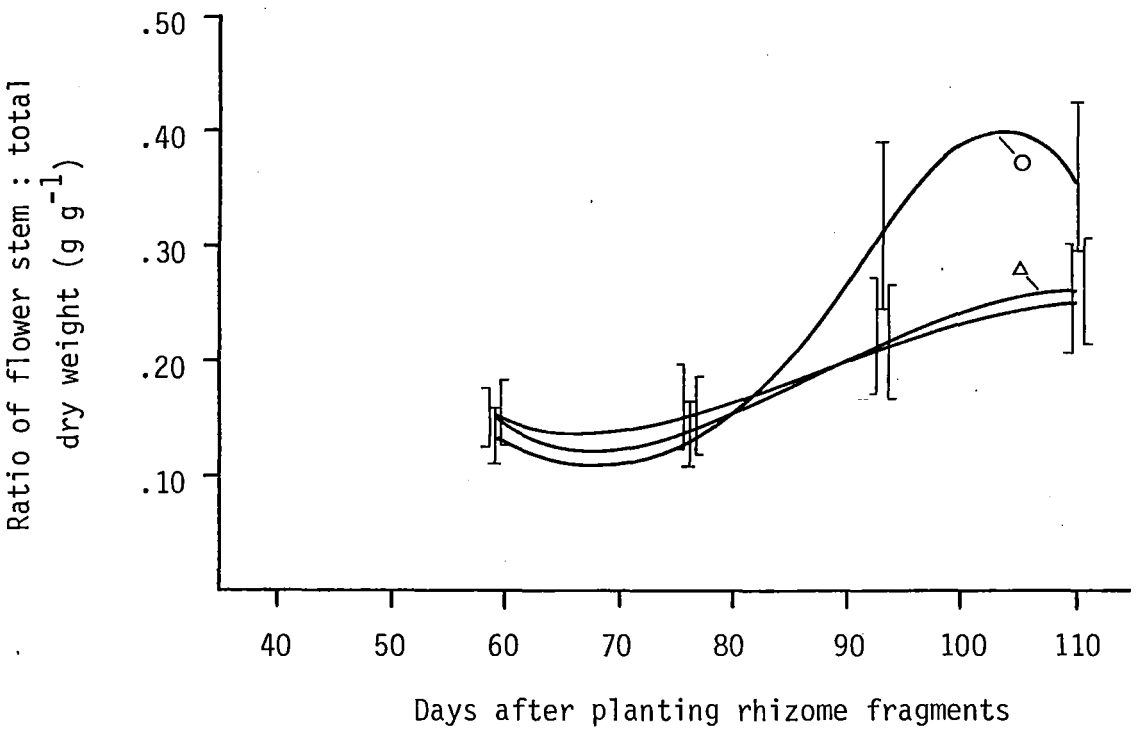


Figure 4.20 Progress curves of yarrow stem dry weight : total dry weight ratio derived from fitted curves of $\log_e S$ and $\log_e W$ (harvests 2 to 5) by subtraction. Bars are the confidence limits for the derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species.

o—— , —— , Δ—— , represent barley densities of 0, 194 and 359 plants m^{-2} respectively.

barley densities (Fig. 4.20). Therefore, in the presence of barley, the yarrow population allocated less of its total dry matter to stem tissue, an effect which would have been partially due to the absence of stem formation by many individuals in the population (Fig. 4.17) and possibly also to a change in allocation within individuals.

Table 4.7 Regression equations for $\log_e$ yarrow stem dry weight m^{-2} (S). t in days from planting rhizome fragments; S in g.

barley density (plants m^{-2})	
0	$21.522 - 0.92460t + 0.012978t^2 - 0.000053698t^3$
194	$7.421 - 0.30501t + 0.004401t^2 - 0.00001844t^3$
359	$6.739 - 0.27195t + 0.003792t^2 - 0.000015398t^3$

4.3.2.8 Barley stem height The growth in height of the barley crop as measured from the soil surface to the base of the youngest fully expanded leaf, followed a sigmoidal pattern, increasing rapidly until harvest 3 (day 76) and then remaining nearly constant (Fig. 4.21). There was no effect due to yarrow, but the barley crop at the high density had significantly taller plants than at the low density (Fig. 4.21). By comparing this pattern of stem elongation in barley with the patterns for yarrow in Figure 4.17, it can be seen that the yarrow population in the presence of both densities of barley, was of lower stature until harvest 4 (day 93), when 10% of the yarrow shoots reached up to or beyond the barley leaf canopy with 194 plants m^{-2}, and 5% with 359 plants m^{-2}. By harvest 5 (day 110), these values had increased to 15 and 6% respectively. Thus throughout most of the time during which the barley and yarrow were associated, the yarrow was of lower stature; only near the end of barley growth did a minority of yarrow stems match or exceed the height of the barley.

4.3.2.9 Yarrow seed yield It was not possible to measure the seed output of the yarrow populations because seed maturation and shedding occurred over an extended period. A coarse assessment of seed production was made by weighing the capitula (including receptacle, bracts, seeds and

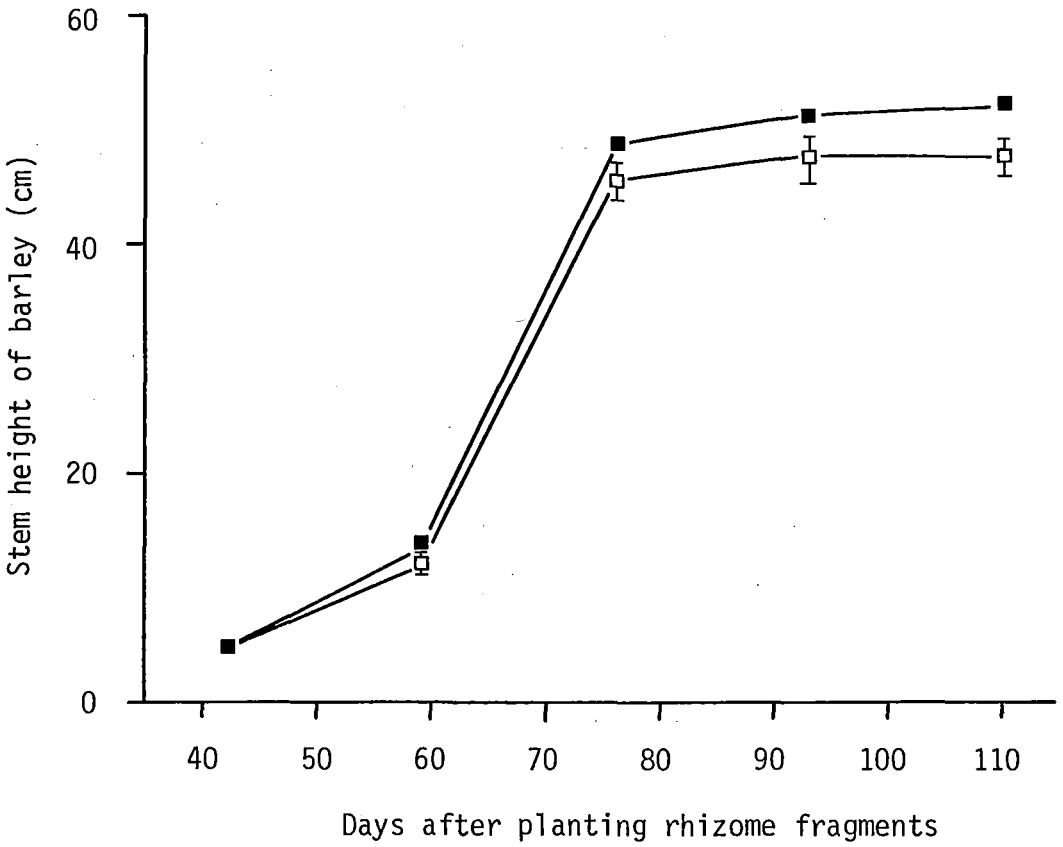


Figure 4.21 Height increase of barley with progress of time. The points are the observed means for 0, 25 and 50 10 cm yarrow rhizome fragments m^{-2}; means of 18 samples, and the bars are the confidence limits (95% probability). □——□, 194 barley plants m^{-2}; ■——■, 359 barley plants m^{-2}.

other floral parts) present on the final harvest (Table 4.8). It can be seen that the presence of barley markedly reduced both the weight of capitula formed by the yarrow population, and the proportion of total dry weight as capitula, and it was inferred that seed production was similarly reduced. Table 4.8 was derived from the data in Appendix XXI.

Table 4.8 -- Main effect of barley density on capitula dry weight of yarrow at harvest 5 (day 110); capitula dry weight as a proportion of total plant dry weight in parenthesis.

barley density (plants m^{-2})	capitula dry weight ($g\ m^{-2}$)
0	126.8 (20.0)
194	5.7 (7.0)
359	2.7 (6.6)
S.E. (Mean)	7.50

4.3.2.10 Barley grain yield Yarrow did not significantly affect the grain yield of the barley crop which was about average for crops in the district (Table 4.9). This table was constructed from the values in Appendix XXII. At the high density of yarrow the number of spikelets ear^{-1}, and grains ear^{-1} were reduced, but this did not bring about a significant fall in grain yield because a compensatory increase in the thousand grain weight occurred. Although there was a trend towards a reduction in the numbers of ears m^{-2}, the differences between the yarrow densities were not significant suggesting that yarrow did not interfer with tillering of the barley.

Table 4.9 Main effect of yarrow on yield components of barley (at 11.7% moisture)

Yarrow density (10 cm rhizome fragments m^{-2})	yield ($kg\ ha^{-1}$)	ears m^{-2}	spikelets ear^{-1}	grains ear^{-1}	1000 grain weight
0	4530 a	671 a	24.0 aA	20.7 aA	41.4 bA
25	4550 a	651 a	23.8 aAB	20.5 aA	42.0 abA
50	4230 a	640 a	23.0 bB	19.4 bA	42.7 aA
S.E. (Mean)	147	22.1	0.23	0.03	0.42

Values within columns, sharing the same letter are not significantly different (Duncans Multiple Range Test); lower case, 5% level; upper case, 1% level.

4.3.3 The growth of yarrow during the autumn and winter

After the final harvest of the barley/yarrow associations and the yarrow alone on 23 February (day 110), five further harvests were made to follow the growth of yarrow during the autumn and winter until the spring. The logarithms of total plant (excluding roots), leaf and rhizome dry weights, and leaf area m^{-2} were described by polynomials as was done in the previous section (4.3.2), following the procedures in Appendices I and II. Again there was no interaction between yarrow and barley density with respect to the measured components (Appendix XII), or between yarrow, barley and time (Appendix XIII) and so, as was done in section 4.3.2, the mean of both yarrow densities was taken to assess the autumn/winter growth of yarrow, and the residual effect of the previous barley crop.

4.3.3.1 Total dry weight The total dry weight of the yarrow populations previously grown with (suppressed populations) and without barley (pure population) increased during the autumn and winter period and the residual effect of the barley was pronounced throughout this period (Fig. 4.22). A decline in total dry weight had occurred by 2 May (day 178) in the pure population as a result of the senescence of flower stems, cauline leaves and seed-shed, and again in the early spring. The autumn decline was not evident in the suppressed populations because only a few stems had been formed and these had been removed (above 12 cm) at the time of harvesting the barley (13 March).

Table 4.10 Regression equations for $\log_e$ yarrow total dry weight m^{-2} (W) during the autumn and winter. t^a in days after planting rhizome fragments; W in g.

previous barley density (plants m^{-2})	
0	$12.013 - 0.082543t + 0.0004000t^2 - 0.000000609t^3$
194	$-8.073 + 0.160779t - 0.0006409t^2 + 0.000000860t^3$
359	$-2.639 + 0.079606t - 0.0002738t + 0.000000337t^3$

a, In these growth curve equations, $t = t_1 - 17$, where t_1 is the time in days after planting the rhizome pieces; t_1 is presented on the bottom axis of these growth curve figures and the curves of the derived functions. It is necessary to subtract 17 from t_1 before substitution in the equations because the values of t used in computation of the equations were 17 days less than they should have been.

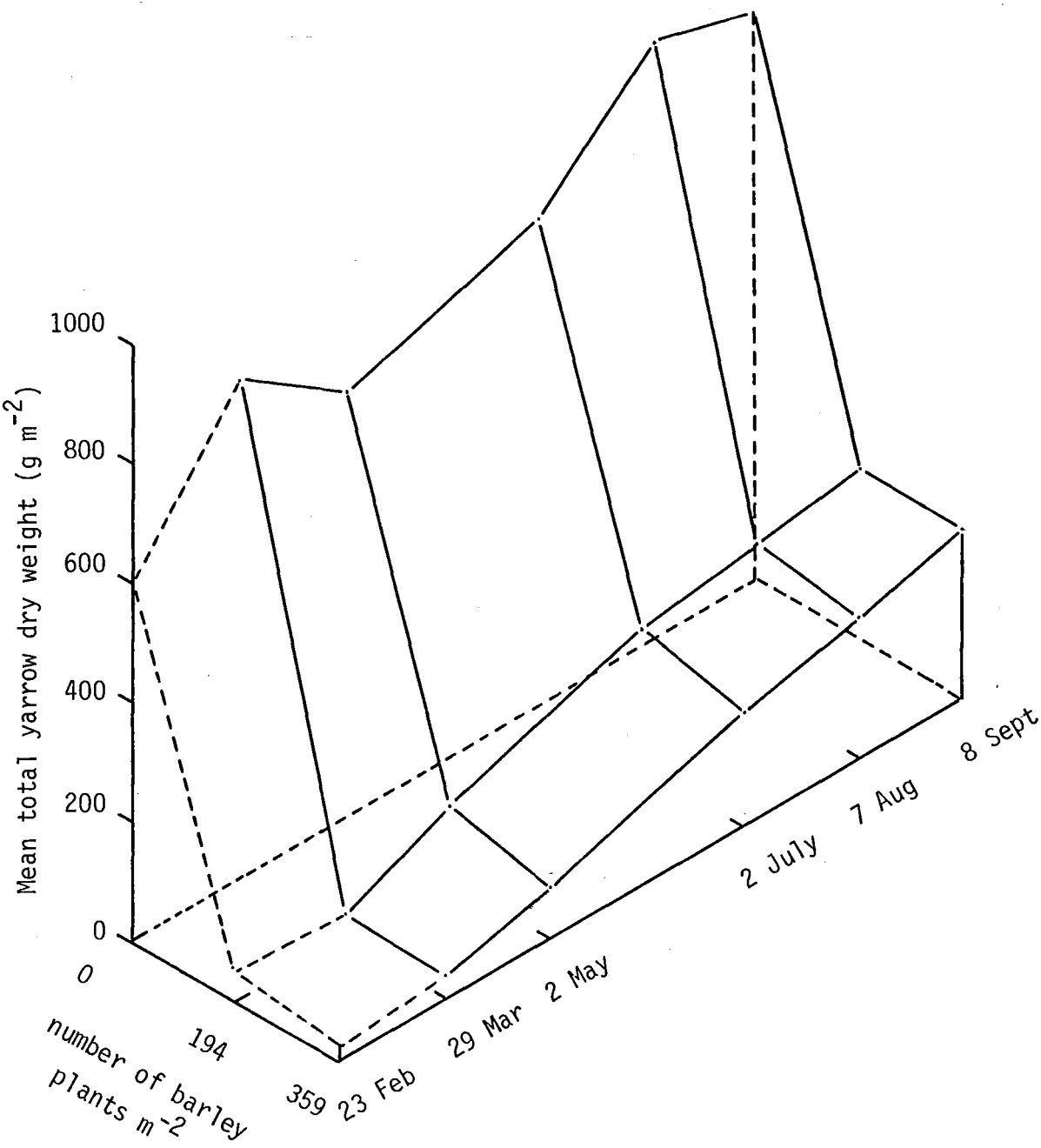


Figure 4.22 The relationship of total dry weight of yarrow to time and density of the preceding barley crop. Points are the backtransformed, observed means of the logarithms for both yarrow densities; the means of 12 samples.

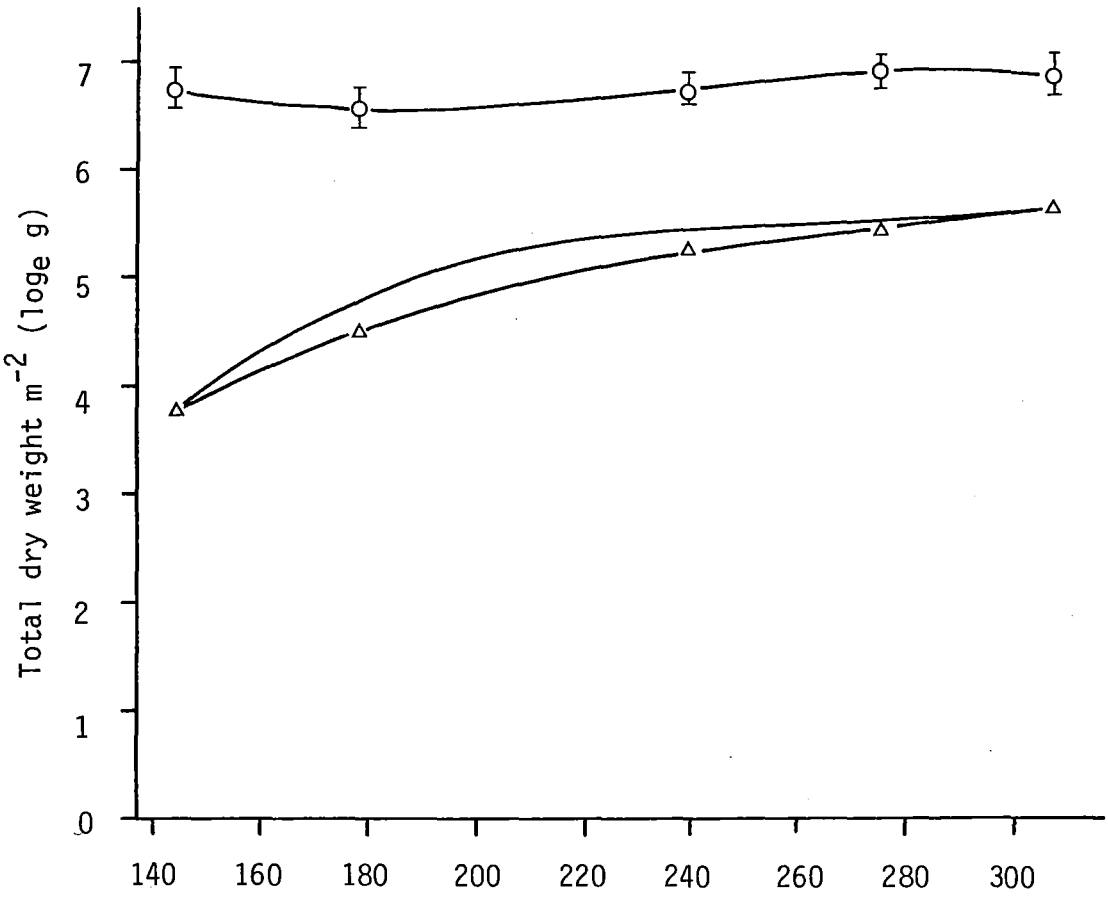


Figure 4.23 Progress curves of yarrow total dry weight m^{-2} during autumn and winter. Points are the observed means of the logarithms for both yarrow densities; means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves. o——o, ——, △——△, represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

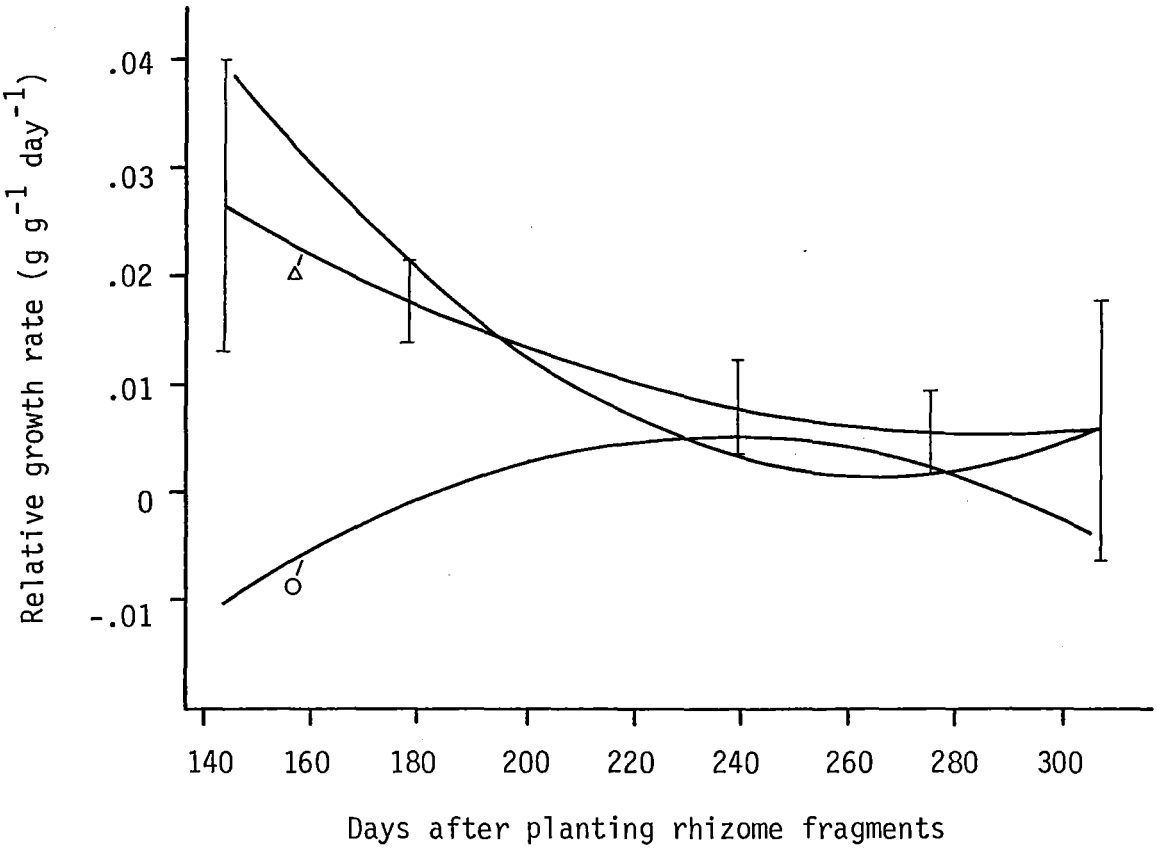


Figure 4.24 Progress curves of relative growth rate of yarrow total dry weight during autumn and winter, derived by differentiation of Figure 4.23. The bars are the confidence limits of the fitted values (95% probability), applying equally to the three curves. o—— , ——, Δ—— , represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

Cubic polynomials adequately described the changes with time in the logarithms of total dry weight (see Appendix XI for measured means) during this growth period (Table 4.10) and the growth curves are illustrated in Figure 4.23. It is evident from Figure 4.23 that the residual effects of both densities of barley, on total dry weight were significant throughout the period, but there was not a significant difference between the weights at 194 and 359 barley plants m^{-2}. The relative growth rates of total dry weight (RGR_W) were significantly higher in the suppressed populations until some time in June (about day 200), showing that these populations were growing more efficiently during this period (Fig. 4.24). This was in marked contrast to the situation when barley was growing with the yarrow; the RGR_W being significantly reduced (Fig. 4.3). As a result of this more efficient growth, the suppressed populations were able to accumulate more dry matter during the period from 29 March (day 144) until 8 September (day 307), despite having entered the autumn with substantially less total dry matter (Figs. 4.22; 4.23).

4.3.3.2 Leaf area A satisfactory fit to the logarithms of the leaf areas (means given in Appendix XI) of the populations was obtained with cubic polynomials (Table 4.11), and these are presented in Figure 4.25. The populations previously grown with barley had significantly less leaf area throughout the autumn and winter, but there was not a signficant difference due to the density of the previous barley. Leaf areas declined throughout the period in the pure populations, but in contrast, increased sharply in the suppressed populations until early June (about day 200), after which a decline similar to that in the pure population occurred. The efficiency of formation of leaf surface was greater in the suppressed populations during the autumn as indicated by the significantly greater relative growth rate of leaf area (RGR_A) during this period (Fig. 4.26). It is also clear from Figure 4.26, that leaf area production fell sharply during the autumn in the suppressed populations, and was negative during the winter, as it was throughout in the pure population.

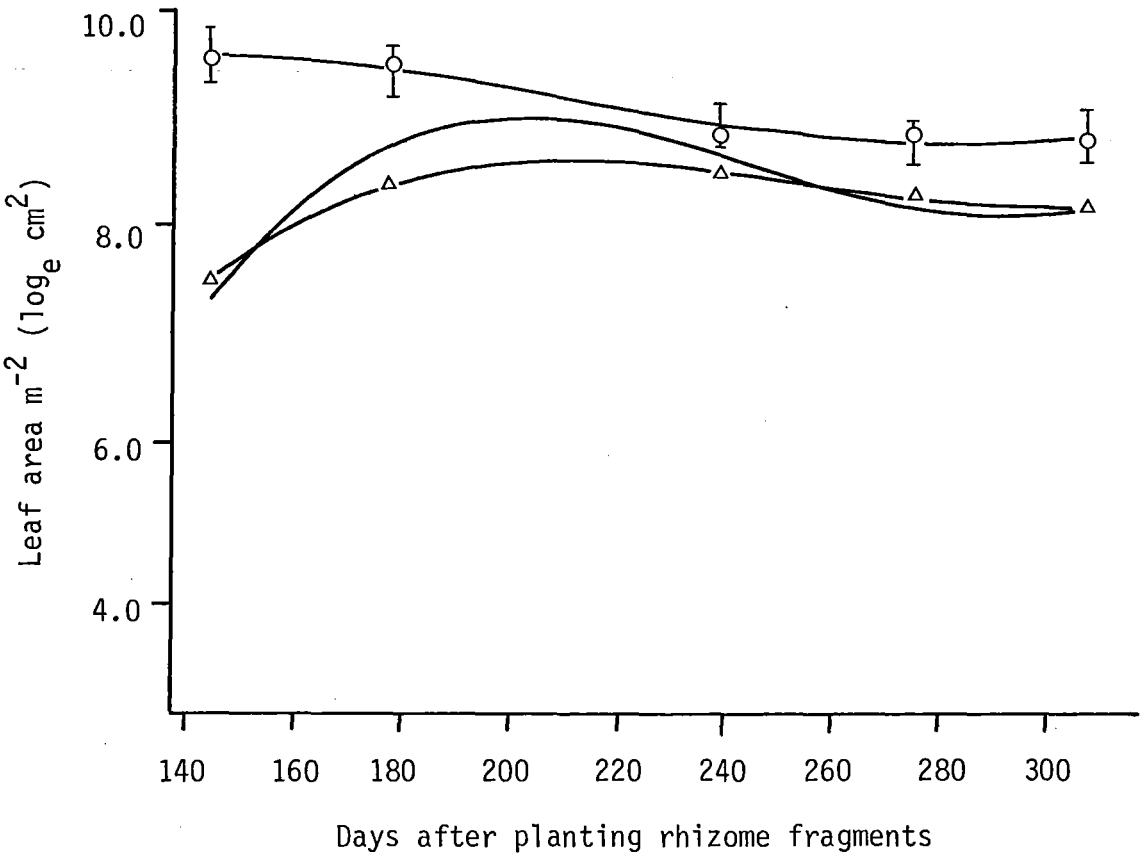


Figure 4.25 Progress curves of yarrow leaf area m^{-2} during autumn and winter. The points are the observed means of the logarithms for both yarrow densities; means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves. o——o, ——, Δ——Δ, represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

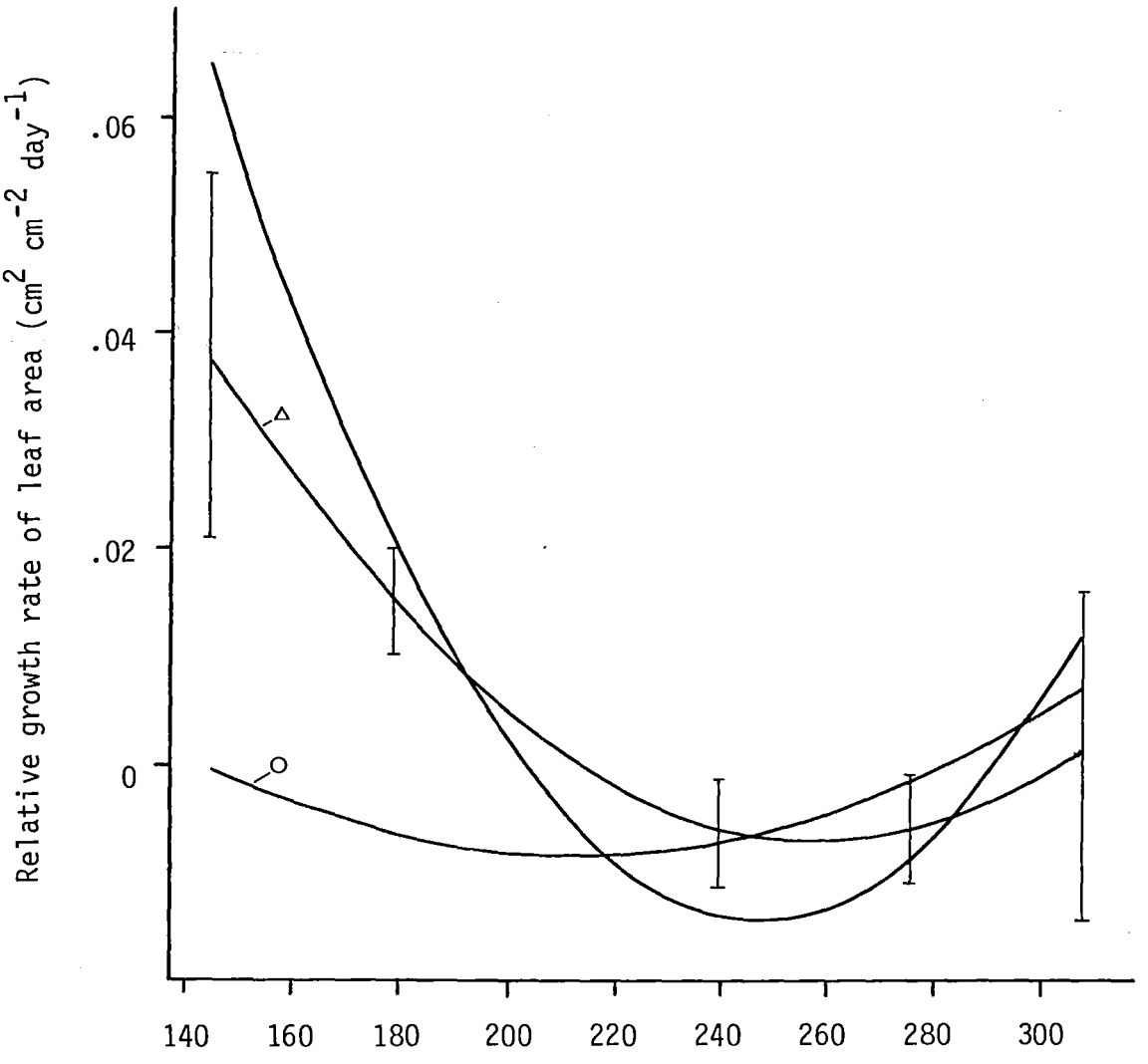


Figure 4.26 Progress curves of relative growth rate of yarrow leaf area during autumn and winter, derived by differentiation of Figure 4.25. The bars are the confidence limits of the fitted values (95% probability), applying equally to the three curves. ○——, ——, △——, represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

Table 4.11 Regression equations for $\log_e$ yarrow leaf area m^{-2}(A) during the autumn and winter. t^a in days after planting rhizome fragements; A in cm^2.

previous barley density (plants m^{-2})	$\log_e$ A
0	$6.551 + 0.057301t - 0.0003367t^2 + 0.000000575t^3$
194	$-18.360 + 0.379306t - 0.0017077t^2 + 0.000002468t^3$
359	$-6.035 + 0.193602t - 0.0008314t^2 + 0.000001147t^3$

a, see Table 4.10

4.3.3.2 Leaf dry weight The progress of the logarithms of leaf dry weights were adequately described by cubic polynomials (Table 4.12) and these are graphed in Figure 4.27. The leaf dry weight followed similar time-trends to leaf area, and was affected in a similar manner by association with barley (Fig. 4.27 cf., 4.25). The observed means are given in Appendix XI.

Table 4.12 Regression equations for $\log_e$ yarrow leaf dry weight m^{-2} (LW) during the autumn and winter. t^a in days after planting rhizome fragments; LW in g.

previous barley density (plants m^{-2})	$\log_e$ LW
0	$3.724 + 0.027539t - 0.0001845t^2 + 0.000000328t^3$
194	$-18.722 + 0.315042t - 0.0014174t^2 + 0.000002055t^3$
359	$-5.249 + 0.112969t - 0.0004695t^2 + 0.000000636t^3$

a, see Table 4.10

4.3.3.4 Net assimilation rate The net assimilation rate (NAR) of the suppressed yarrow populations was significantly higher until early June (about day 200) than in the pure population, but during the rest of the winter, the populations had similar NARs (Fig. 4.28). There was no difference caused by the density of the previous barley.

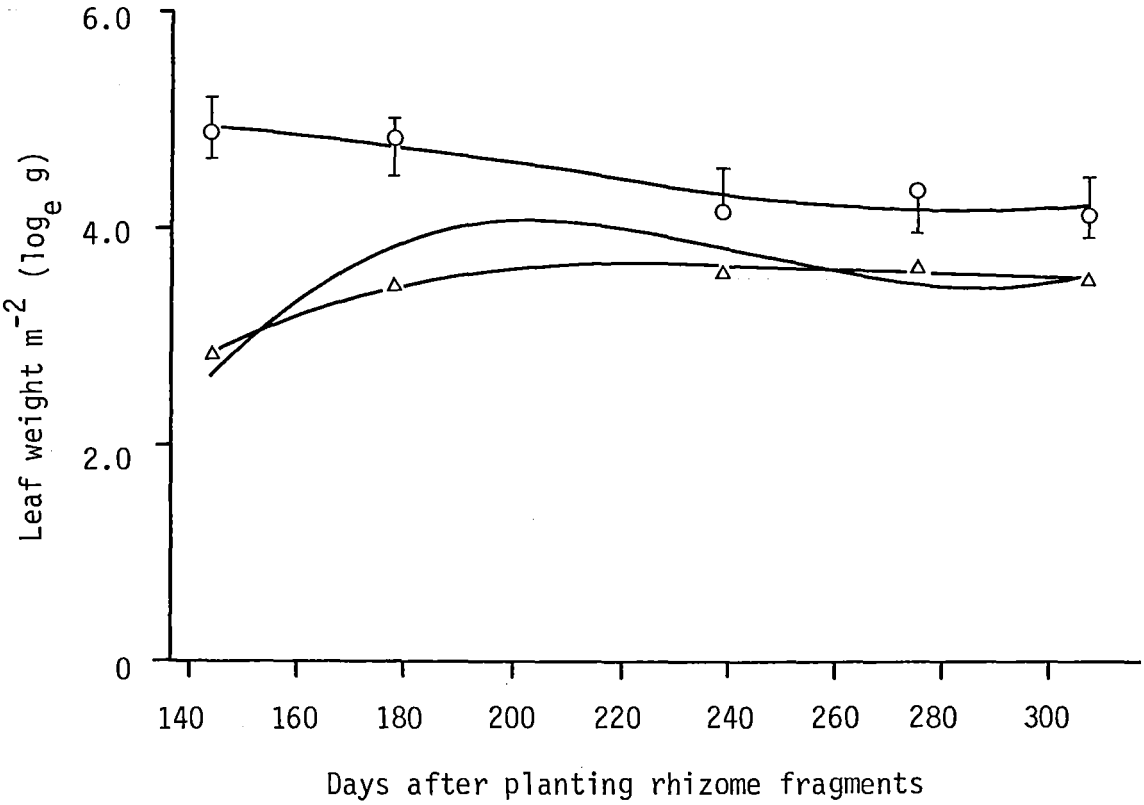


Figure 4.27 Progress curves of yarrow leaf dry weight m^{-2} during autumn and winter. The points are the observed means of the logarithms for both yarrow densities; means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves. o——o, ——, Δ——Δ, represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

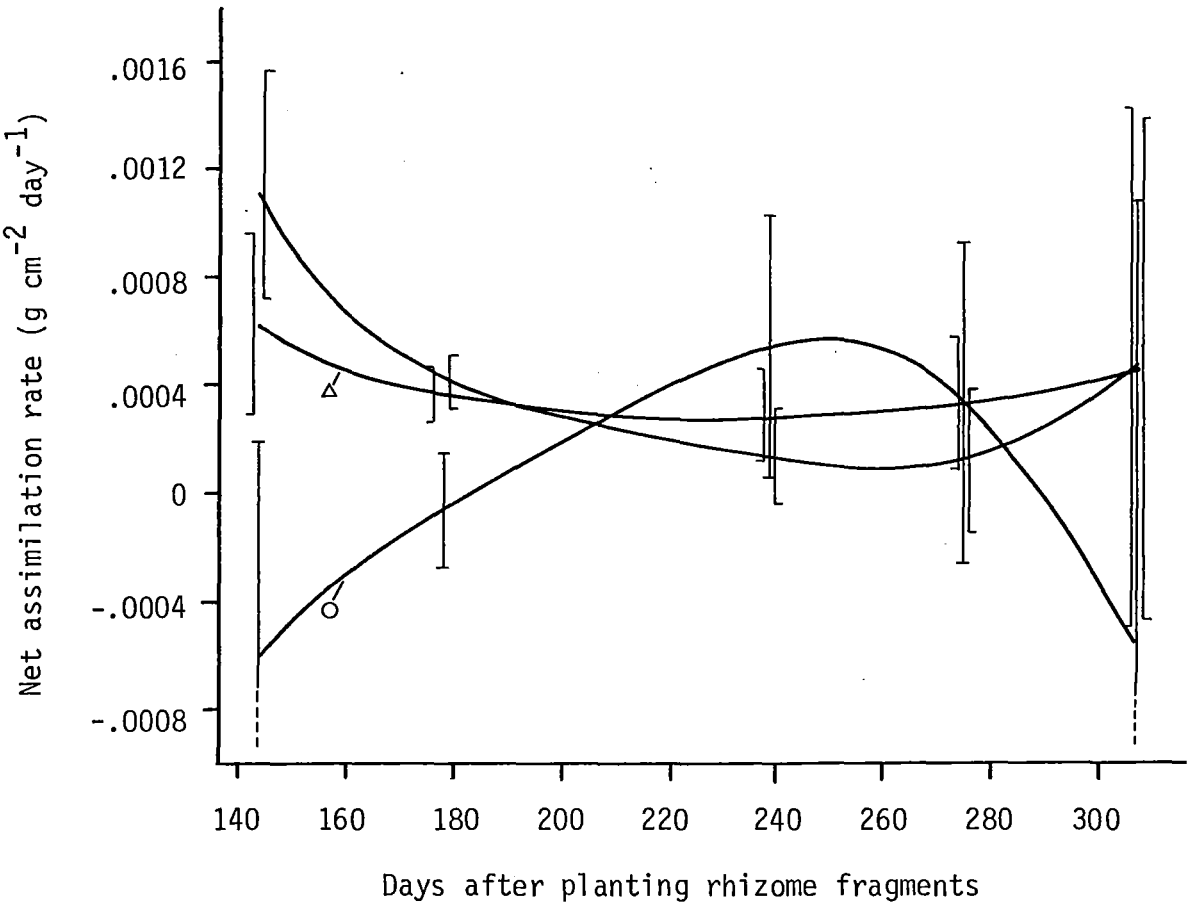


Figure 4.28 Progress curves of yarrow net assimilation rate during autumn and winter, derived from fitted curves of $\log_e W$ and $\log_e A$ by differentiation and division. Bars are the confidence limits for the derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. o—— , —— , Δ—— , represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

Negative NARs in the autumn and early spring in the pure population (Fig. 4.28) were associated with the loss in total dry weight during these periods (Fig. 4.22; 4.23; 4.24).

4.3.3.5 Leaf area ratio; specific leaf area; leaf weight ratio
The LARs of the suppressed populations were significantly higher than in the pure populations throughout the autumn and winter, and declined with time after an initial rise during March (Fig. 4.29). At the time of the first autumn/winter harvest (day 144, 34 days after removal of the barley), the SLAs were the same in all yarrow populations, but there was a rapid rise until June in the SLAs of the suppressed populations, followed by a decline back to the original values, while the SLAs of the pure population altered little with time (Fig. 4.30). On the other hand, the LWRs of the suppressed populations were approximately twice as high on day 144, and remained higher throughout the period, while the LWR of all populations declined with time (Fig. 4.31).

4.3.3.6 Rhizome growth The rhizome systems of the yarrow populations increased in dry weight during the autumn and winter and the residual effect of the barley was marked (Fig. 4.32). There was a decline in the dry weight of the rhizomes in the pure population in early August which brought about the decline in total dry weight at this time (Fig. 4.22), and which was possibly due to reserve depletion by the emerging rhizome apices in the spring. However, if this was the case, it is difficult to explain why this decline did not also occur in the suppressed populations.

Table 4.13 Regression equations for $\log_e$ new yarrow rhizome dry weight m^{-2} (R) during the autumn and winter. t^a in days after planting rhizome fragments; R in g.

previous barley density (plants m^{-2})	$\log_e R$
0	$5.069 - 0.029189t + 0.0002820t^2 - 0.000000582t^3$
194	$-16.515 + 0.248642t - 0.0009639t^2 + 0.000001265t^3$
359	$-20.064 + 0.294453t - 0.0011754t^2 + 0.000001595t^3$

a, see Table 4.10

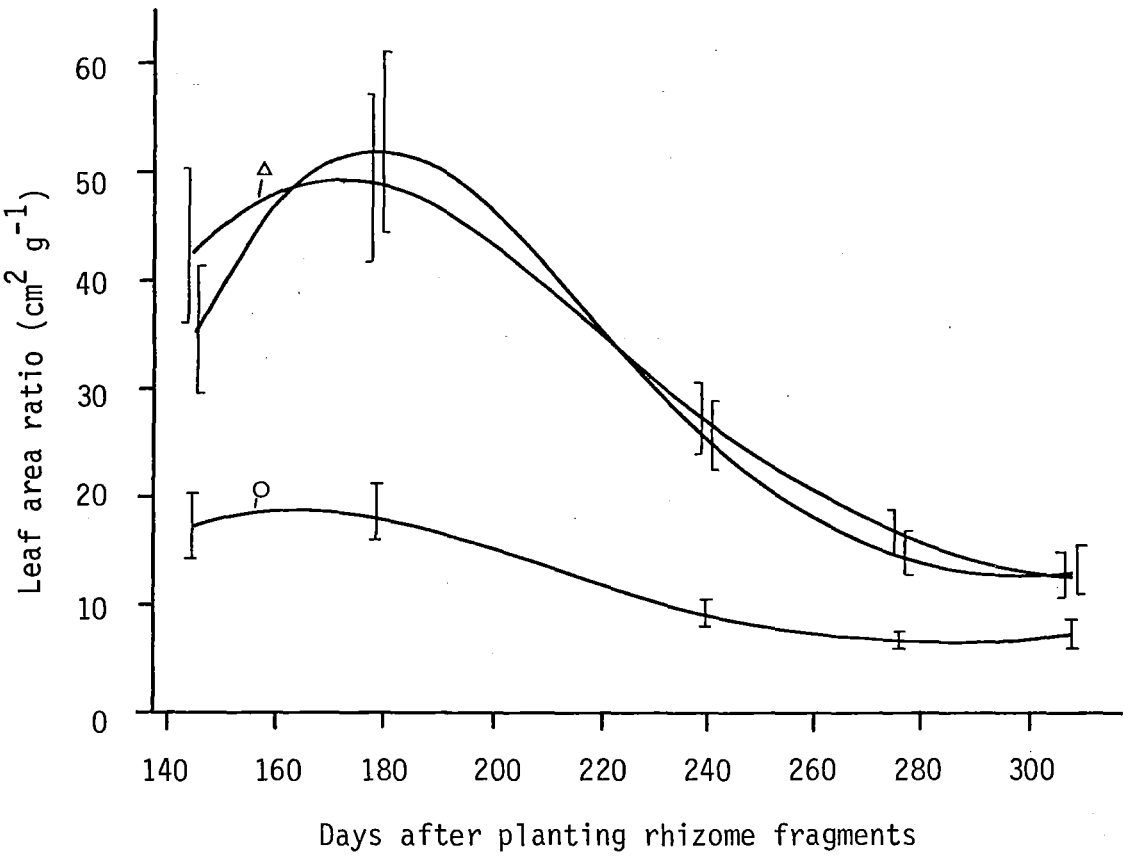


Figure 4.29 Progress curves of yarrow leaf area ratio during autumn and winter, derived from fitted curves of $\log_e A$ and $\log_e W$ by subtraction. Bars are the confidence limits for the derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. o—— , —— , Δ—— , represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

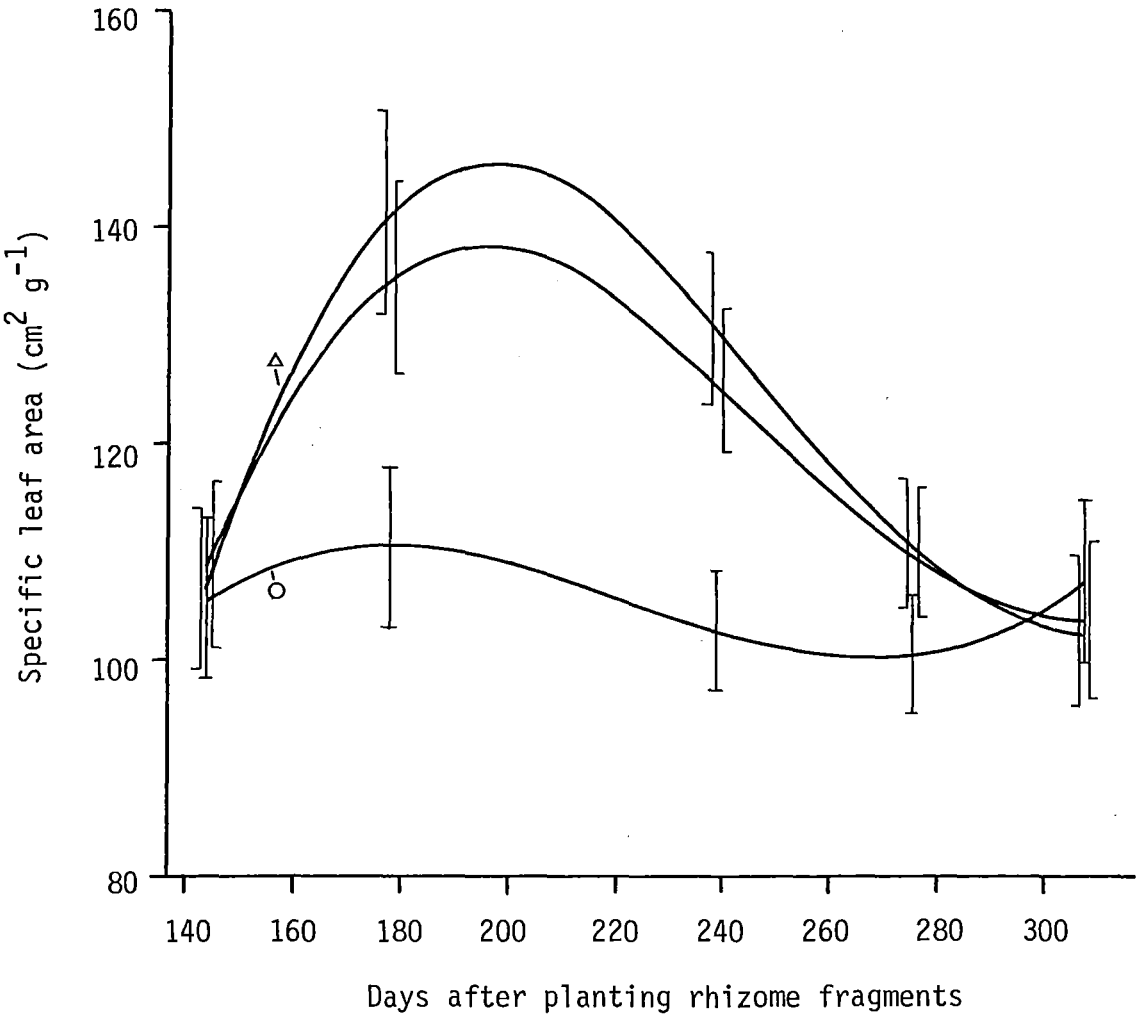


Figure 4.30 Progress curves of yarrow specific leaf area during autumn and winter, derived from fitted curves of $\log_e A$ and $\log_e LW$ by subtraction. Bars are the confiddence limits for the derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. o—— , ——, Δ—— , represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

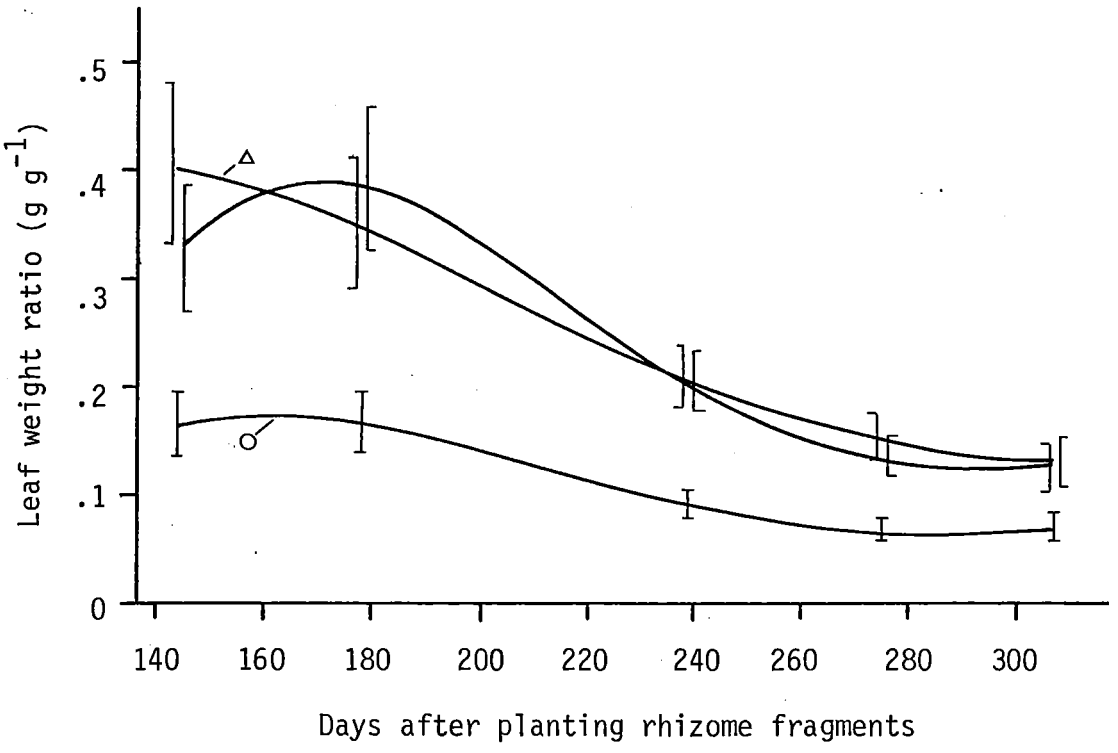


Figure 4.31 Progress curves of yarrow leaf weight ratio during autumn and winter, derived from fitted curves of $\log_e LW$ and $\log_e W$ by subtraction. Bars are the confidence limits for the fitted values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. o—— , ——, Δ—— , densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

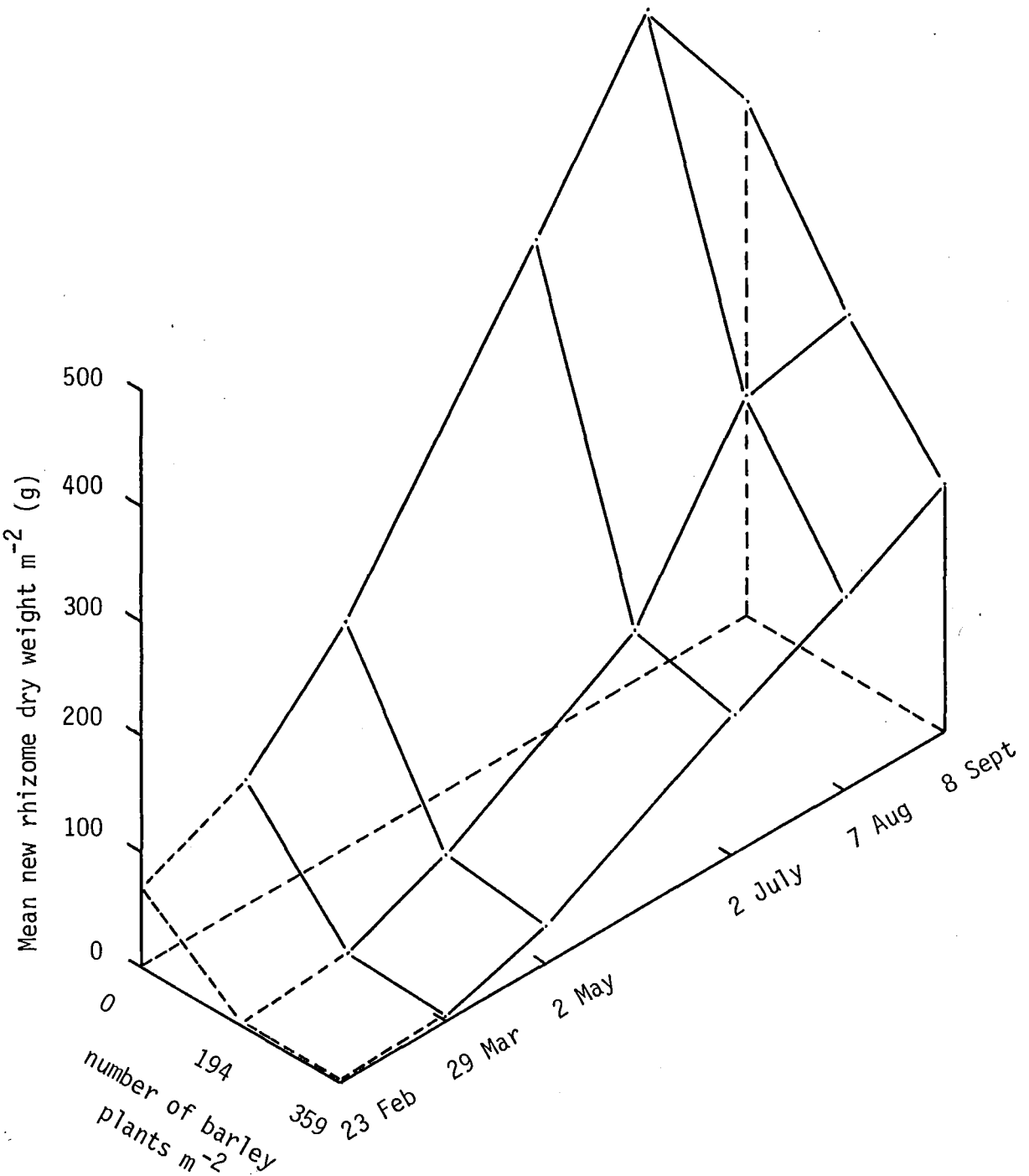


Figure 4.32 The relationship of new rhizome dry weight to time and density of the preceding barley crop. Points are the backtransformed, observed means of the logarithms for both yarrow densities; means of 12 samples.

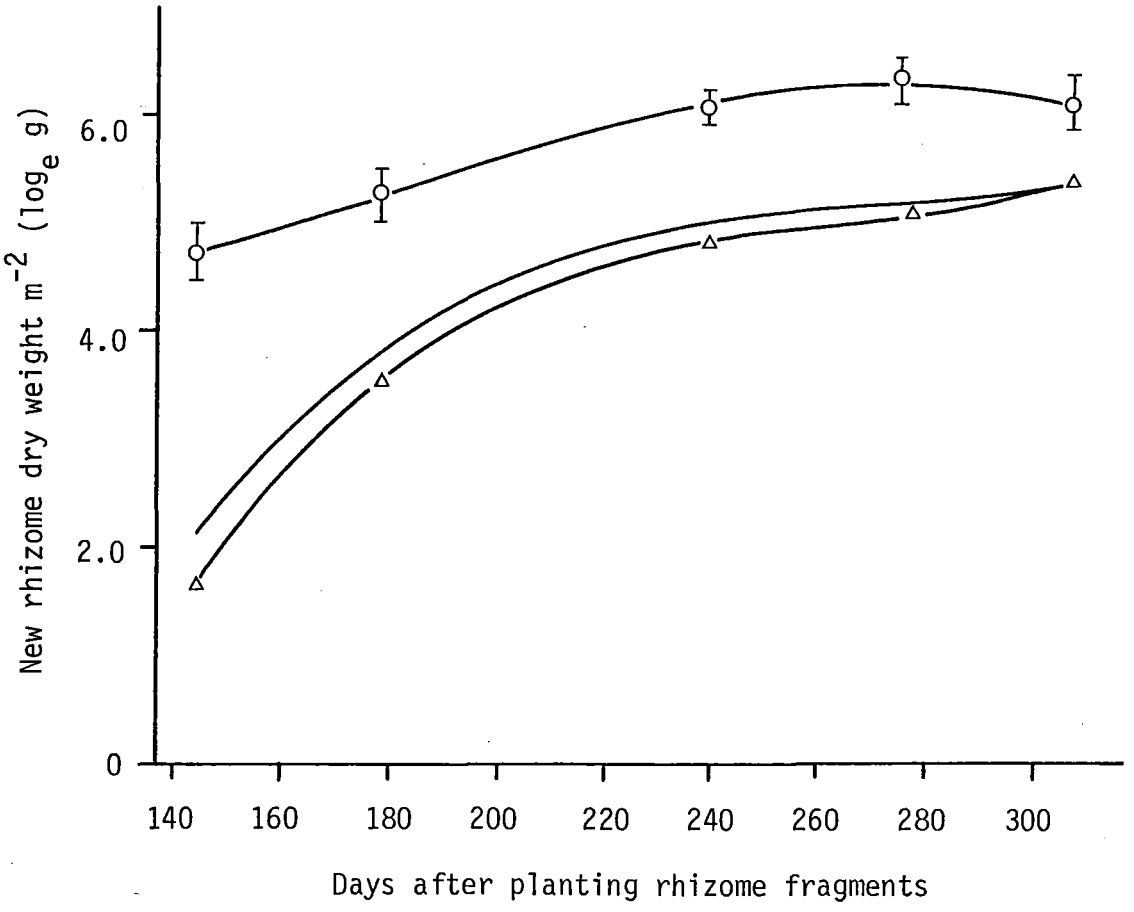


Figure 4.33 Progress curves of new rhizome dry weight m^{-2} during autumn and winter. Points are the observed means of the logarithms for both yarrow densities; means of 12 samples. The lines are the curves fitted to all individual samples and the bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves. o——o , ——, Δ——Δ , represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

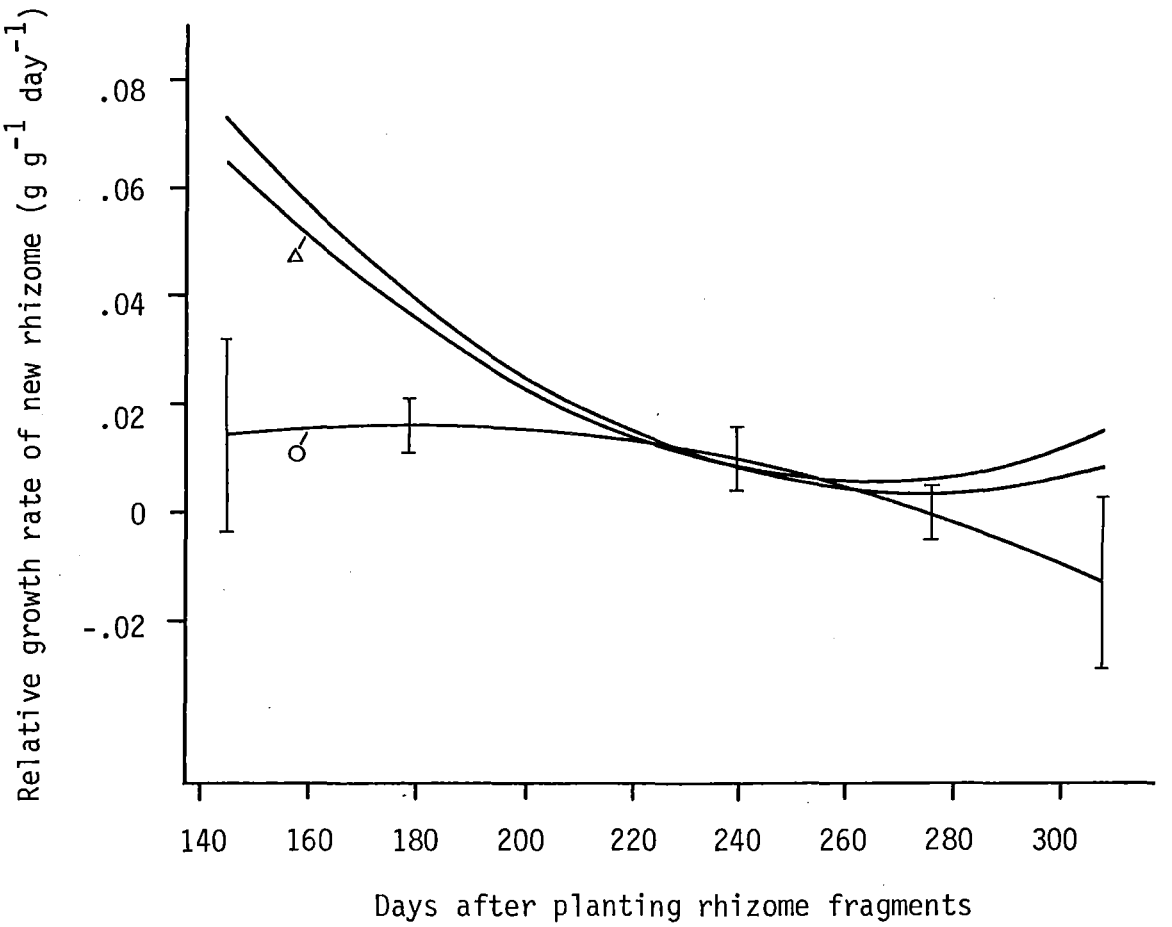


Figure 4.34 Progress curves of new rhizome relative growth rate during autumn and winter, derived from Figure 4.33 by differentiation. The bars are the confidence limits for the fitted values (95% probability), applying equally to the three curves. o—— , ——, Δ—— , represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

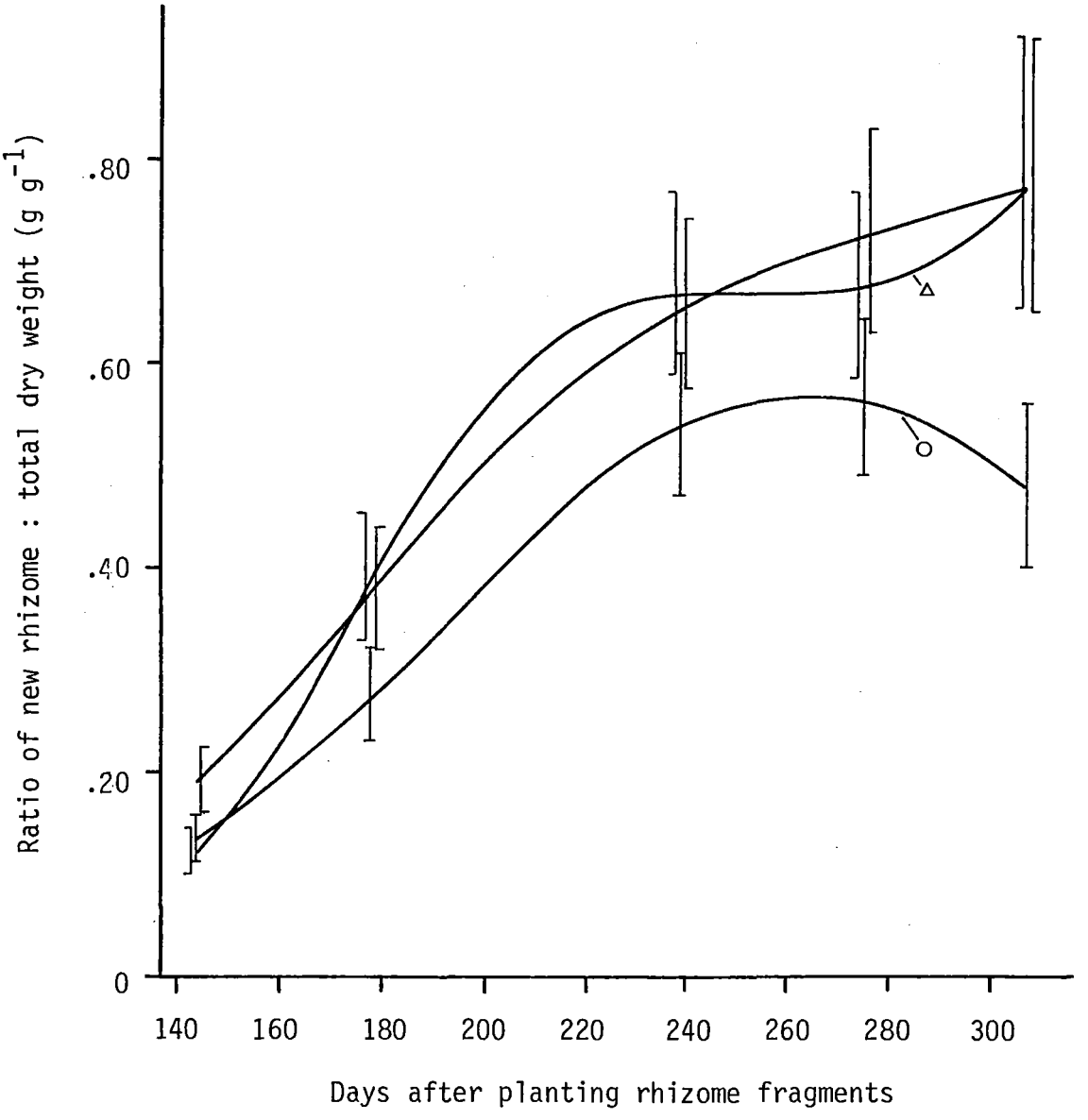


Figure 4.35 Progress curves of new rhizome dry weight : total dry weight ratio derived from fitted curves of $\log_e R$ and $\log_e W$ (Figures 4.33 and 4.23) by subtraction. Bars are the confidence limits for the derived values (95% probability), and are presented to the right and left of the points on the curves to which they apply, in the case of the low and high density respectively, of the associate species. o—— , ——, Δ—— , represent densities of preceding barley crop of 0, 194 and 359 plants m^{-2} respectively.

The trends in the logarithms of rhizome dry weight (observed means given in Appendix XI) were suitably described by cubic polynomials (Table 4.13) and the curves are plotted in Figure 4.33, from which it can be seen that the suppressed populations had significantly less rhizome dry matter throughout the autumn and winter period. However, the relative growth rate of rhizome dry matter (RGR_R) was significantly higher in the suppressed populations until early June (Fig. 4.34), and as a result, these populations were able to produce a similar amount of rhizome dry matter during the autumn and winter as the pure population (Fig. 4.32). Because of this more efficient rhizome growth during the autumn by the suppressed populations, the amount of rhizome dry matter in these populations, as a percentage of that in the pure populations became greater with time and in this sense, the suppressed populations were 'catching up' on the pure populations. On 29 March (day 144), the yarrow population which had been associated with 359 barley plants m^{-2} had only 4.6% of the rhizome dry matter of the pure population, but by 8 September (day 307) this had increased progressively to 48%. In contrast, during the presence of the barley, at 359 plants m^{-2}, the amount of rhizome dry matter as a percentage of the amount on the pure population declined from 20% on 3 January (day 59) to 1.7% on 23 February (day 110) as a result of the significant barley-induced reduction in the RGR_R (Fig. 4.13).

The importance of rhizome production during the autumn and winter by the yarrow populations can be seen in the rapidly increasing rhizome weight ratios (RWR) (Fig. 4.35). By 8 September (day 307) the suppressed populations had allocated 77% of their total dry matter production to the formation of rhizomes. The pure population however, had 47% of its total dry matter as rhizome on 8 September, significantly less than the suppressed populations.

4.4 DISCUSSION

Growth analysis of the yarrow populations was performed with the dry weight of the planted rhizome fragments included in the total dry weight. It was considered necessary to include the fragments because they

formed a considerable sink for photosynthate during the experimental period; trebling in dry weight between day 59 and day 100 without barley, and increasing one and a half times in the presence of 194 and 359 plants m^{-2} (Appendices XXIV and XXV). However, it may be argued that the original dry weights of the planted fragments should have been subtracted from the total plant dry weight at all harvests to allow a more meaningful interpretation of the results in terms of the efficiency of current growth. This is biologically sound and therefore to investigate the consequences, an estimate of the original dry weight of the fragments was deducted from the total dry weights at each harvest and the mean values of the growth analysis parameters, for the four inter-harvest periods, were compared with those calculated before excluding the estimate (Table 4.14). The estimate of the original dry weight of the planted fragments was obtained by separately weighing 50 individual pieces selected at random from the material to be planted. The mean dry weight 10 cm $fragment^{-1}$ was 0.15 g $\pm$ .043 (one standard deviation).

The SLA is clearly independent of the total plant dry weight, but LWR and therefore LAR are quite dependent upon the total weight. When the estimate of the original weight was subtracted, the LARs on 17 December (day 42) became considerably higher, and biologically untenable values were obtained for the population in the presence of barley (Table 4.14). These unusually high LARs were clearly the result of the very small new estimates of total dry weight, indicating that the estimate of the original mean fragment weight was by chance, higher than the true mean. However the effect of subtracting this weight was reduced with time as it formed a decreasing proportion of the total dry weight. It will also be seen that the LARs were consistently higher in the presence of barley, but had a more correct estimate of the original dry weight been available and deducted, it would be expected that the increase in LAR in the presence of barley would have been less. The changes brought about in the LAR upon exclusion of the original dry weight estimate were clearly entirely due to changes in the LWR (Table 4.14).

The $\overline{RGR}$s in the first inter-harvest period were considerably higher with the estimate of the original weight subtracted as a result of the greater proportional reduction in total dry weight on day 42 than

Table 4.14 A comparison of growth analysis components of yarrow with, and without the original dry weight of the planted rhizome fragments included in the total dry weight.

sampling date	days	barley density (plants m^{-2})	W ($g\ m^{-2}$)	W- 5.625† ($g\ m^{-2}$)	LAR (+) ($cm^2\ g^{-1}$)	LAR (-) ($cm^2\ g^{-1}$)	LWR (+) ($g\ g^{-1}$)	LWR (-) ($g\ g^{-1}$)	$\overline{LAR}$ (+)	$\overline{LAR}$ (-)	$\overline{LWR}$ (+)	$\overline{LWR}$ (-)	$\overline{RGR}_W$ (+) ($g\ g^{-1} day^{-1}$)	$\overline{RGR}_W$ (-) ($g\ g^{-1} day^{-1}$)	$\overline{NAR}$ (+) ($g\ cm^{-2}\ day^{-1}$)	$\overline{NAR}$ (-) ($g\ cm^{-2}\ day^{-1}$)	RWR (+) ($g\ g^{-1}$)	RWR (-) ($g\ g^{-1}$)	SWR (+) ($g\ g^{-1}$)	SWR (-) ($g\ g^{-1}$)
17 Dec.	42	0	7.149	1.524	29	137	.257	1.21	Means for consecutive inter-harvest periods are registered beside the second harvest date for each period.											
		194	5.641	0.016	28	9,929	.204	71.89												
		359	5.818	0.193	29	864	.207	6.23												
3 Jan.	59	0	23.23	17.61	50	66	.540	.713	40	102	.399	.962	.069	.144	.00173	.00141	.045	.060	.132	.174
		194	17.24	11.62	51	76	.502	.745	40	5,003	.353	36.3	.066	.388	.00165	.000078	.023	.034	.151	.224
		359	14.12	8.50	47	78	.475	.789	38	471	.341	3.51	.052	.223	.00137	.000473	.015	.025	.147	.244
20 Jan.	76	0	103.89	98.26	56	59	.476	.503	53	63	.508	.608	.088	.101	.00166	.00160	.072	.076	.135	.143
		194	32.25	26.62	63	76	.538	.652	57	76	.520	.699	.037	.049	.00065	.00064	.034	.041	.148	.179
		359	21.83	16.21	51	69	.447	.602	49	74	.461	.696	.026	.038	.00053	.00051	.020	.026	.154	.207
6 Feb.	93	0	330.86	325.21	55	56	.411	.418	56	58	.444	.461	.068	.070	.00121	.00121	.118	.120	.297	.303
		194	47.23	41.61	59	67	.463	.526	61	72	.501	.589	.022	.026	.00036	.00036	.056	.064	.208	.236
		359	29.57	23.95	52	64	.415	.513	52	67	.431	.558	.018	.023	.00035	.00034	.022	.027	.216	.267
23 Feb.	110	0	604.44	598.82	29	29	.257	.259	42	43	.334	.339	.035	.036	.00083	.00084	.119	.120	.358	.362
		194	51.27	45.65	40	45	.358	.402	50	56	.411	.464	.005	.005	.00010	.00009	.053	.059	.256	.287
		359	36.59	30.97	39	46	.343	.406	46	55	.379	.460	.013	.015	.00028	.00027	.032	.038	.249	.294

†, mean dry weight of planted rhizome fragments in $g\ m^{-2}$ (mean dry weight $fragment^{-1}$ = .15 g); (+), calculated using W; (-), calculated using W - 5.625; W, total plant dry weight ($g\ m^{-2}$).

$\overline{LAR} = LAR_2 + LAR_1/2$; $\overline{LWR} = LWR_2 + LWR_1/2$; $\overline{RGR} = \log_e W_2 - \log_e W_1/t_2 - t_1$; $\overline{NAR} = \overline{RGR}/\overline{LAR}$, where t is time in days after planting the rhizome fragments.

on day 59 (Table 4.14). However, the increase in $\overline{RGR}$ was much greater in the presence of barley due to the greater proportional reduction in the initial dry weights in these populations, and the $\overline{RGR}$ became higher in the presence of barley. In the subsequent inter-harvest periods, exclusion of the original weight estimate made little difference to $\overline{RGR}$, although the relative reduction due to barley was marginally less (Table 4.18).

As a result of the very high estimates of $\overline{LWR}$ and hence $\overline{LAR}$ in the first period, after subtraction of the initial weight, the estimate of the $\overline{NAR}$s by $\overline{NAR} = \overline{RGR} \div \overline{LAR}$ were much lower (Table 4.14). In subsequent periods, exclusion of the initial weight made very little difference to either the magnitude of $\overline{NAR}$ or the relative differences between $\overline{NAR}$ of populations without and with barley.

Similar patterns were evident with RWR and SWR (Table 4.14), there being little absolute difference after the first period upon exclusion of the estimate of original weight, and no substantial alteration of the effect of barley, except for slightly lower percentage reductions in the ratios in the presence of barley.

It has been seen that when deducted from the total dry weight, the apparently over-estimated original dry weight of planted rhizome pieces resulted in exceptionally small estimates of the total plant dry weight produced by current photosynthesis by 17 December (day 42). This lead to biologically unreasonable values of LWR and LAR (Table 4.14). Furthermore, even if the original dry weight of the planted fragments had been more accurately known, subtraction of this value at each harvest would still not have accounted for loss of weight by the fragments resulting from decay.

On balance then, it was considered defensible to include the original weight of the planted rhizome fragments in the total plant dry weight, recognising the LWRs and RGRs were almost certainly underestimated by the fitted curves during the first inter-harvest period, and that the relative changes in these components in the presence of barley were similarly underestimated during this period. However, with the progress of time and the reduction in the proportion of total dry weight attributable

to the original weight of planted fragments, the consequences of including this initial weight became insignificant.

When two species emerge at or near the same time, such as weeds in cereal crops, the degree of success of either species depends largely on its size at emergence, its relative growth rate, and its time scale from emergence relative to that of the other species (Milthorpe, 1961). Density is also an important factor (Dew, 1972; Wells, 1979) as is the growth habit of the competing species. Hammerton (1962) found that the differences in the competitive ability of three species of *Polygonum* towards kale (*Brassica oleracea*) reflected their growth habit; *P. aviculare* was less competitive than *P. lapathifolium* and *P. persicaria* because it was placed at a distinct disadvantage with regard to light interception owing to its prostrate habit, whereas the latter two species had erect, branching habits and were considerably more competitive.

The importance of seed size (initial capital) has been demonstrated by Black (1958). In a comparison of two cultivars of *Trifolium subterraneum*, the larger seeded type succeeded in competition with a type with smaller seeds because it was able to form a larger leaf surface and hence was able to obtain a larger proportion of the available light. Similarly, Aspinall and Milthorpe (1959) and Aspinall (1960) showed that barley (*Hordeum vulgare*) succeeded in association with white persicaria (*Polygonum persicaria*) despite its lower RGR because of its larger embryo size, giving larger plants at emergence, with larger root systems. The divergence between the amount of growth of the two species with time led to the white persicaria plants becoming progressively more and more shaded, which ultimately caused a further reduction in the rate of root system and leaf expansion.

Differences between competing species in the rates and pattern of morphological development may have profound effects on the final outcome of an association. Harper and Clatworthy (1963) found that although *Trifolium fragiferum* had larger seeds and larger cotyledonary areas than *Trifolium repens*, the greater hypocotyl elongation and more rapid leaf production in *T. repens* seedlings resulted in a larger and more effective photosynthetic surface and early dominance by this species. However, *T. fragiferum* was finally successful in the association because it remained

vegetative longer and continued to produce new leaves on petioles above the *T. repens* canopy.

If the weight of the planted rhizome fragments (5.6 g m^{-2}) and of grain (13.0 g m^{-2}) be considered as the initial capitals of the mean yarrow and barley populations respectively, it is apparent that the barley began with more than twice the capital of the yarrow population. However these are over-estimates of the true starting capital by as much as the proportion of the rhizome and grain weights not consumed in the formation of the young shoot and root systems. This will have been considerably greater in the yarrow than in the barley, making the true difference in initial dry weights greater than indicated by the difference between planted grain and rhizome dry weights. In spite of this, and having produced only 52% as much dry matter as the barley population by day 42, the pure yarrow population had produced 72% as much total dry matter as the pure barley by day 110 (Figs. 4.2, 4.1a and b). These similar yields were achieved by considerably different patterns of growth, which essentially reflected the annual and perennial nature of the two species. The barley population had produced approximately 50% of its final (day 110) yield by day 76 (20 January) whereas the yarrow had formed only 17% of its yield at day 110 (Fig. 4.2), patterns of growth which resulted from the high initial RGR of the barley population, which fell steeply with time, and the lower but more stable RGR of the yarrow, which was higher than in the barley from day 59 (Fig. 4.3).

These differences in the time related changes of the RGR between the two species were attributable predominantly to differences in ontogenetic changes in the LARs rather than NARs. Until about day 80, the pure yarrow population had a higher NAR than the pure barley population (Fig. 4.7a cf., 4.7b), but in both populations the rates remained substantially constant until this time, and therefore contributed little to the changes in RGR. On the other hand, the LAR of the barley population was initially much higher than in the yarrow, but declined more rapidly with time (Fig. 4.8). A breakdown of the LAR into LWR and SLA revealed the barley population to have had initially over 80% of its total dry weight in leaf tissue, whereas the yarrow had little more than

20% (Fig. 4.10), and in the barley population, there was a greater leaf surface per gram of leaf tissue (Fig. 4.9). The combination of this greater allocation of total dry matter to leaf tissue, and the greater expansion in space of each gram of leaf tissue resulted in the higher initial LAR and hence higher RGR of the barley population. However, the barley population did not maintain this high level of leafiness and high RGR because the allocation of dry matter to leaf tissue dropped markedly throughout the growth period, most probably as a consequence of the increasing allocation to stem and reproductive growth with time, and leaf senescence in the later part of growth as shown by the negative RGR_A after day 70 (Fig. 4.5). Furthermore, changes with time in the spatial distribution of leaf dry matter occurred in the barley population which caused the leaves to become thicker until day 55, after which they became thinner during stem elongation and early grain formation, with a further decline in SLA during grain filling (Fig. 4.9). These changes in SLA, which were probably largely ontogenetic, also contributed to the marked fall in the LAR of the barley population with time.

The SLA of the pure yarrow population followed a similar drift with time and was always lower than in the barley population (Fig. 4.9), but the yarrow population was able to maintain a higher RGR for a longer period because it maintained a much higher proportion of its total dry matter as leaf tissue (Fig. 4.10). This was aided by the lack of leaf senescence until day 100 (Fig. 4.5), the maintenance of a high RGR_A, and despite the formation of rhizomes, flower stems and reproductive organs, which formed an increasing proportion of the total dry weight with time (Figs. 4.16, 4.20).

In summary, although the yarrow population began with much less dry matter than the barley population, it was able to produce almost as much total dry matter by the time of the final harvest (day 110), because it maintained a relatively stable RGR throughout the period, in contrast to the barley population, which made rapid early growth but only slow growth in the later part of the period. These differences were attributable mainly to differences in morphogenetic factors governing the distribution of total dry matter to leaf production, the expansion of this leaf dry matter in space, and to the vastly different ontogenetic drifts.

Competition, the restriction in growth that arises from association with other plants, must result from a change in one or more factors of the local environment of the plant. Light, mineral nutrients, and water are the factors which are most likely to be involved, and the relative importance of these factors may vary with time in an association. Pavlychenko (1940) considered that competition begins as soon as the root system of one plant invades a feeding area of another, usually taking place long before the tops are developed sufficiently to exert serious competition for light. Aspinall (1960) found restricted nutrient supply was the factor which first decreased the growth of white persicaria (*Persicaria lapathifolium*) associated with barley (*Hordeum vulgare*), while competition between shoots for light became important later in the association.

The SLA of the yarrow populations followed a complex ontogenetic drift, similar to that of the barley, but less marked. The decline in SLA until the beginning of stem extension (day 59, Fig. 4.9) has also been shown to occur in spaced seed-propagated plants (Fig. 3.17) and probably represents an increase in leaf thickness with age. The following rise in SLA with the onset of stem formation also confirms similar findings in Chapter 3, and in the present case was probably a response to self shading within the pure population and shading by the barley in the suppressed population. In Chapter 3, self shading was considered to occur in spaced plants when a total dry weight of 4.5 g plant^{-1} was reached (Fig. 3.20 d) and it might have also been expected to occur at this weight in the present experiment. A total weight of 4.5 g plant^{-1} was reached just after day 80 in the pure population (Fig. 4.1 a), and if an allowance be made for the exclusion of roots and the inclusion of planted rhizome fragments, it seems likely that the upturn of SLA may have coincided with a total dry weight of about 4.5 g, and thus could reasonably be ascribed to self shading.

In the early stages of the experiment, the SLA of yarrow was higher in the presence of barley, indicating that the plants were being shaded. However, contrary to expectation, during the rising phase of SLA (day 60 - 75) and also during its final decline, the SLAs were the same in the pure and suppressed populations. At first this seems to

indicate that the suppressed population was not being shaded by the barley in the middle and late stages of the association, but this hardly seems possible. The SLA is a measure of the expansion of the leaf tissue of the whole plant (population) in space and as such its value is an integration of the values of all individual leaves. It was apparent that the light intensity received by different leaves in the pure population depended upon their position on the plant; those at the base of flower stems, on vegetative apices of primary shoots and emerged rhizome shoots and basal second order axes were clearly being shaded by the higher leaves on the flower stems as they were showing the marked elongation typical of shaded leaves (Fig. 3.5). The upper cauline leaves were apparently in an environment of higher light intensity than the lower leaves. Similarly, in the yarrow associated with barley, the leaves originating from ground level were in a distinctly less favourable light environment than the middle and upper cauline leaves. Therefore it seems that the similarity between the SLAs in the presence and absence of barley during the stage of yarrow stem formation, can be explained on the basis of self shading in the pure population, and shading by the barley in the suppressed population.

Although the yarrow was clearly being shaded by the barley from the time of the first harvest, it is not possible to conclusively attribute the reduction in RGR_W to shading. In Chapter 3 it was shown that yarrow is able to maintain its RGR_W down to a light level of 50 to 60% full daylight and that a marked reduction would not be expected until levels fell below 30% (Fig. 3.23, 3.22) due to the inverse relationship between NAR and LAR. However, in the present experiment, the RGR_W of the yarrow had apparently fallen by the time the light levels beneath the barley had been reduced to 51 and 37% of full daylight at 194 and 359 barley plants m^{-2} respectively (Fig. 4.3), due to reduction in NAR (Fig. 4.7 a) without the expected adaptation of LAR (Fig. 4.8). The lack of any adaptation of LAR was caused by a decline, rather than the expected increase in LWR (Fig. 4.10). The data in Table 4.15 however do suggest that had a good estimate of the original rhizome dry weight been available and deducted from the total dry weight, then the LWR and hence LAR would have shown the expected increase

associated with shading, and there may well have been no real decline in the RGR_W in the early part of the studied growth period. Further discussion of the growth analysis results during this first harvest interval would be hazardous for reasons already outlined, suffice to suggest that if the reduction in RGR_W was real, then some factor other than light was most certainly involved.

During the remainder of the experimental period, the RGR_W of yarrow was depressed in the presence of barley, entirely as a result of reduced NAR (Fig. 4.3, 4.7 a) and as already explained, the SLAs of populations with and without barley were similar, indicating that both populations experienced similar overall light intensity. If this was the case then it would seem that some factor other than light was limiting the NAR of the yarrow. Competition for mineral nutrients was possibly the cause of the reduction in NAR during the middle phase of the association; a water shortage being unlikely as the whole trial area was irrigated on 11 November, 10 January and again on 21 January. Watson (1952) showed changes in NAR can occur with changes in nutrient supply while Thurston (1959) was able to increase the NAR of *Avena fatua* and *A. ludoviciana* by increasing the nitrogen supply.

In the late phase of the association (6 to 23 February) when the barley was in the grain ripening stage, the soil had dried out considerably and some yarrow plants were seen to be wilting in the presence of barley. Reduction in water has been known to substantially interfere with assimilation efficiency. Leaf desiccation was shown to cause a marked inhibition of the photosynthetic activity per unit area of leaf (Hsiao, 1973) and Boyer and McPherson (1975) found desiccation of maize (*Zea mays*) caused a marked reduction in gross photosynthetic activity due to changes in chlorplast level and stomatal activity. Furthermore, leaf enlargement can be reduced by only small degrees of desiccation and is generally affected long before photosynthesis as a result of a lack of turgor for cell enlargement (Boyer and McPherson, 1975). As well as the reduction in NAR, the yarrow population in the presence of barley also had a markedly reduced relative rate of leaf expansion (RGR_A, Fig. 4.5) and it is suggested that water may have been the limiting factor for yarrow growth in the later stage of the association.

The growth analysis presented here has demonstrated the complex and dynamic nature of growth of yarrow and barley populations and how very different they are from one another. When growing together, the inherently lower initial RGR_W of the yarrow population put it immediately at a disadvantage with the faster-growing and more numerous barley plants, from which it was unable to recover in the continued presence of the barley. It appeared that some factor other than light, possibly restricted nutrient supply, as a consequence of the rapid early exploitation of the soil by the barley root systems, first reduced the rate of growth of the yarrow. Consequently many plants were unable to emerge from the rosette form and were further restricted in growth within the rapidly growing barley population. The growth of these vetetative individuals was probably restricted also by the low light levels at the base of the barley, but the SLA of the population as a whole seemed to react in a way which suggested that overall, the suppressed population was receiving a similar amount of light as the pure population.

Rhizome production by the yarrow population was markedly suppressed in the presence of barley (Fig. 4.11) due to reduced initiation and reduced subsequent growth (Fig. 4.12). More importantly from the point of view of the plant as a weed capable of regenerating from rhizome pieces, the percentage of total dry matter production allocated to rhizomes was reduced in the presence of barley (Fig. 4.16), indicating that a higher degree of stress imposed by a more competitive crop could possibly reduce the vegetative reproductive effort to zero. This would clearly be desirable in a programme to control yarrow. Sexual reproductive effort was also markedly reduced (Table 4.8) in the suppressed yarrow population as a consequence of both reduced stem formation (Fig. 4.17) and reduced growth of stems which were formed (Fig. 4.19) and again, greater competitive stress may completely prevent flowering in a population. Indeed, this was shown to be possible by Bourdôt and Butler (unpublished) when they were able to prevent both new rhizome and flower stem formation in a natural population by sowing a spring barley crop immediately after the final cultivation. In contrast to the present experiment, regrowth shoots did not emerge until after the barley, which presumably resulted in more severe competition towards the slow-growing yarrow rosettes.

The growth analysis showed that yarrow did not interfere with the accumulation of dry matter by the barley, which was clearly the strongest competitor of the two species in this experiment, as a result of its high initial RGR_W and greater initial weight, in spite of emerging later than the yarrow. The grain yield was consequently not altered in the presence of the yarrow and was about average for the district. No significance was attached to the slight, although statistically significant variations in some grain yield components.

During the presence of barley, the efficiency of growth of the yarrow population was markedly reduced, but in the autumn and early winter, after the removal of the barley, the suppressed yarrow population had a higher RGR_W than the pure population (Fig. 4.24). This resulted in a greater absolute increase in total dry matter between 29 March and 8 September in the suppressed yarrow (Fig. 4.22). On 23 February, the NARs of the yarrow population with and without barley were similar (Fig. 4.7 a) but on 29 March, 34 days after removal of the barley, the suppressed populations had significantly higher NARs than the pure population. This was the result of both an increase in the suppressed population during the 34 days after removing the barley, and a decrease during this period in the pure population (Fig. 4.7 a cf., Fig. 4.28). Release of the yarrow population from the competitive stress previously imposed by the barley was probably the main reason for the increase in NAR in this population, but it is also possible that the removal of the senescing flower stems with the barley lowered the respiration rate of the whole population which would have effected an increase in the NAR. The NAR of the pure population was negative until early May (Fig. 4.28) as a consequence of the high respiration rate which must have accompanied the senescence of stems and floral structures, but increased and became positive in early May when the rate of dry matter increase exceeded any continued loss by senescence. From early June until early September, the pure and suppressed populations had similar and low (although positive) NARs presumably owing to the cold temperatures and low light conditions at that period of the year.

The LARs of the suppressed populations were higher than in the pure population throughout the autumn and winter (Fig. 4.29) as a conseq-

uence of both a greater allocation of total dry matter to leaf tissue (Fig. 4.31) and a greater expansion of the tissue (Fig. 4.30). This generally greater leafiness of the suppressed population over this period, in combination with the higher NARs in the autumn resulted in the greater RGR_W of the suppressed populations during the autumn (Fig. 4.24) and was associated with a much higher rate of leaf expansion (Fig. 4.26). Higher rates of leaf production and expansion were possible in the suppressed populations because of the high proportion of vegetative apices remaining in these populations and probably less inter-plant competition between these relatively small plants. It is possible that the decaying barley residues provided a fertility boost to the suppressed yarrow, which could partly explain the higher efficiency of growth of these populations.

As a corollary to the greater efficiency of overall growth in dry matter during the autumn in the suppressed population, rhizome dry matter production was also more efficient (Fig. 4.34), and consequently the residual effect of the competition provided by the barley, declined with time over this period (Fig. 4.32).

The analysis presented here has shown that a relatively low density yarrow population, regenerating from rhizome fragments was able to produce almost as much biomass by late February as a spring sown barley crop, but was a poor competitor with the barley as a result of slow initial growth. The reproductive effort (vegetative and sexual) was reduced in the presence of barley and it was considered that seed and rhizome production could be completely inhibited with greater competition as might be provided by ensuring that the barley emerged before the yarrow. The high degree to which the yarrow population was suppressed emphasised the importance of suitably competitive crops for preventing a rapid increase in rhizome and seed reserves in the soil, and the vigorous growth of rhizomes during the autumn and winter after removal of the crop demonstrated the rapidity with which the competitive effect on rhizome production can be negated.

CHAPTER 5

THE RHIZOME SYSTEM AND ITS REGENERATIVE POTENTIAL

5.1 INTRODUCTION

Seasonal variations in regeneration of roots, rhizomes and other vegetative organs have been found to occur in several species. In an investigation of the propagation of 12 species from root cuttings, Graham (1936) found that five regenerated best before flowering, three after flowering and two in the flowering month and another month. Only two species were most efficient only during the month of flowering. Also, when propagating 12 species from stem cuttings, 5 regenerated most efficiently before flowering, 5 after flowering, but only 2 species were best during the flowering month. Root cuttings of the raspberry (*Rubus idoeus*) showed a marked seasonal fluctuation in regenerative ability, with the greatest percentage success occurring in cuttings taken during the winter months (Hudson, 1953). Dore (1953) demonstrated seasonal variation in the regenerative capacity of root cuttings of horse-radish (*Armoracia rusticana*); regeneration was poor during the flowering period. In Wisconsin, Johnson and Buchholtz (1962) showed that the buds on rhizome fragments of couch (*Agropyron repens*) had a low regenerative capacity during the late spring, even though favourable conditions for growth were provided. This period of innate bud dormancy, 'late spring dormancy', was subsequently shown to occur in Britain by Leaky, Chancellor and Vince-Prue, (1977 a). Hakansson (1963) found that although many of the bulbs and bulbils produced by *Allium vineale* sprouted in the late summer and autumn following their formation, some did not grow until the following spring while others remained dormant for 5 years or more. A period of innate dormancy was shown to occur during late summer and autumn in rhizome sections of Western Ironweed (*Vernonia baldwinni*) and in root cuttings of leafy spurge (*Euphorbia esula*) by Monson and Davis (1964). This dormancy was apparently broken naturally in the field by low soil temperatures. The existence of a recurring cycle of high and low activity in the rhizomes of *Vernonia baldwinni* was confirmed by Davis and McCarty (1966).

Other studies have also demonstrated seasonal variations in regeneration of vegetative organs. Lipke, Burnside and Haskins (1965) showed that bud activity on single-node rhizome fragments of tanweed

(*Polygonum coccineum*) was lowest during the months of flowering and increased to 100% during the following spring. Parker (1966) found that *Cirsium arvense* was difficult to establish from small excised root and underground stem fragments in mid-summer, but much easier in spring. The regenerative ability of root fragments of leafy spurge (*Euphorbia esula*) was lowest in the summer at the time of maximum flowering (Raju *et al.* 1964) Henson (1969) investigated a range of temperate species and found a number to have distinct periods in the year during which regeneration and vigour of regenerating plants was low. Species showing poor regeneration during the autumn/winter included; *Calystegia sepium*, *Sonchus arvensis*, *Mentha arvensis*, *Aegopodium podagraria*, *Cardraria draba*, *Rorippa sylvestris* and *Tussilago farfara*. Stem and root fragments of *Convolvulus arvensis* on the other hand, had a low regenerative capacity in summer and regenerated most readily in the winter (Henson, 1969, 1971). *Achillea millefolium*, although showing no distinct seasonality, appeared to regenerate most poorly in the winter (Henson, 1969). Correlations between flowering periods and low regenerative ability have been ascribed to various factors including changes in hormonal status and redistribution of metabolites. Hakansson (1963) considered that the dormancy of *Allium vineale* bulbs could be the result of poor gas permeability of the outer coverings of the bulbs.

Periods of dormancy do not, however, occur in the vegetative propagules of all plants. No evidence could be found by Chancellor (1967) for a period of reduced bud activity on rhizome fragments of *Polygonum amphibium*, and the buds of Johnsongrass (*Sorghum halepense*) rhizomes maintained a similar degree of regenerative potential throughout the year (Hull, 1970; Horowitz, 1972 a). The percentage sprouting of buds on rhizome pieces of *Cynodon dactylon*, although fluctuating widely during the year, showed no pronounced trend with time (Horowitz, 1972 b).

Seasonal fluctuations of food reserves which may be associated with seasonal changes in regenerative capacity have been demonstrated in several species (Arny, 1932, cited by Henson, 1969). He found that reserves in the subterranean systems of *Convolvulus arvensis*, *Euphorbia esula*, *Nasturtium austriacum* and *Sonchus arvensis* were minimal during spring, subsequently increasing during the summer. Little seasonal variation was found to occur in rhizome reserves of *Agropyron repens*.

Reserves in the roots of *Cirsium arvense* and in the rhizomes of *Tussilago farfara* were found to reach their lowest level during summer and to rise to a maximum in autumn (Bakker, 1960).

Recently Leaky, Chancellor and Vince-Prue (1977 a) found the nitrogen content of the rhizomes of *Agropyron repens* was correlated with the seasonal fluctuations in bud activity. They showed the nitrogen content to be lowest in late spring, the period of inherent bud dormancy as demonstrated by Johnson and Buchholtz (1962). It was suggested that this dormancy resulted from sudden translocation of almost all the available nitrogen out of the old rhizomes, to be utilised in the spring flush of shoot and new rhizome growth. This hypothesis is supported by the earlier work of Dexter (1936) in Michigan in which it was shown that rhizome sections from plants dug from nitrogen-fertilised soil in late spring had a much greater ability to sprout than from unfertilised soil. It was noted that many rhizomes from unfertilised plots appeared to be in perfectly healthy condition but failed to sprout. Further confirmation of the role of nitrogen in the phenomenon of late spring dormancy in the rhizomes of *Agropyron repens* has been given by Leaky, Chancellor and Vince-Prue (1977 b). By increasing the concentration of potassium nitrate to single-node rhizome pieces collected during the period of dormancy, from one to 210 ppm, they were able to release the buds from dormancy. The restoration of regenerative capacity was associated with increased utilisation of rhizome sugars and it was concluded that this dormancy was attributable to a block in soluble sugar utilisation resulting from a lack of nitrogen. Lipke, Burnside and Haskins (1965) obtained a correlation between the percentage of total nitrogen in the rhizomes of *Polygonum coccineum* and bud activity; both were low during flowering and increased to maximum levels in the following spring. The percentage of total nitrogen in the roots of *Convolvulus arvensis* was shown to rise during autumn and fall to a low level in late spring (Frazier, 1943) during which time the roots have been shown to have a low regenerative potential (Henson, 1971).

Seasonal variations have been found in the carbohydrate reserves of a number of perennial species. Barr (1939), in Colarado, revealed that the total carbohydrate, as a percentage of fresh weight in *Cardraria*

draba and *Convolvulus arvensis* was lowest in spring and increased to a maximum in summer followed by a slow decline over the winter months. This pattern of reserve content is positively correlated with the seasonal fluctuations in regenerative capacity shown by Henson (1971); maximum regeneration occurring following the peak in carbohydrate content. Similar fluctuations in the carbohydrate reserves of *Convolvulus arvensis* were found also by Barr (1940) and Frazier (1943).

In general, the literature seems to suggest that root and rhizome reserves may be highest in the late summer/early winter period, apparently having been accumulated during the preceeding months of active growth. Therefore it may be that maximum regenerative capacity often occurs during the winter period as a consequence of ample food reserves, and conversely is restricted at times when rapid new growth may be depleting reserves stored over previous growth periods.

It would seem that such dormancy, induced by restricted reserves can be overcome by increasing the supply of relevant nutrients to the propagules (Leaky, Chancellor and Vince-Prue, 1977 b). Thus this phenomenon is unlikely to occur in soil of high fertility and hence would have limited capability for exploitation in weed control systems. However, in plants where a period of innate dormancy occurs in fragmented propagules, that is not related to nutrient status of the propagule, then this may be able to be exploited for control purposes. For example, the periods of dormancy in *Vernonia baldwinni* and *Euphorbia esula* occurring in late summer/early autumn are broken naturally in the field by low soil temperatures (Monson and Davis, 1964), and Hakansson and Wallgren (1972) have shown that a pronounced dormancy in all parts of the underground root system of *Sonchus arvensis* occurring in late summer/early autumn could be broken by storage at $2^{o}C$ for one month in the winter. It should be possible to take advantage of such a dormant period and the associated delay in emergence of the plants by appropriate timing of cropping. If a crop was sown during the weed's dormant period, the delay in emergence of the weed would put it at a considerable competitive disadvantage with the already established crop.

In addition to the inherent dormancy, which prevents fragments of vegetative propagules from regenerating at certain periods of the year,

correlative inhibition has been shown to occur in the rhizomes of several weedy species. Hull (1970) found rhizome buds of Johnsongrass (*Sorghum halepense*) were strongly inhibited by apical dominance and it has been estimated that 95% of the buds on the rhizomes of *Agropyron repens* remain inactive during the entire life of the rhizome unless it is disturbed by fragmentation (Johnson and Buchholtz, 1962).

It is not completely resolved whether the suppression of lateral rhizome buds by the dominant apex is due to an excess of an inhibitor substance or because of a shortage of essential materials in the form of growth substances (e.g. cytokinin or gibberellin), mineral nutrients (e.g. nitrogen), carbohydrates or water. Evidence supporting an hypothesis that apical dominance is due to competition between the apical bud and the lateral buds for nitrogen (McIntyre, 1965; 1971; 1972; 1977), water (McIntyre, 1971; 1976; Qureshi and McIntyre, 1979) and carbohydrates (McIntyre, 1969; 1971) has been accumulated from studies with *Agropyron repens*. In general, this hypothesis is based on experiments which have shown that hitherto dormant lateral buds can be induced to grow if supplied with nitrogen, adequate water or carbohydrates. Leaky, Chancellor and Vince-Prue (1978 a) suggested that the effects of nitrogen on dominance in rhizome fragments could be explained in terms of competition for nutrients between developing shoots and the antagonistic effects of nitrogen on an auxin-mediated inhibition by the dominant shoot. Leaky and Chancellor (1975) showed that a mixture of 1 - naphthyl acetic acid and 6 - benzylaminopurine could effectively substitute for the apex and maintain lateral bud dormancy if supplied to both ends of rhizome fragments of *Agropyron repens*, suggesting that both parental and apical factors are involved in lateral bud suppression. These authors suggested it is unlikely that the simple competition for nutrients and water as suggested by McIntyre, is the only mechanism for dominance in rhizomes of *Agropyron repens*. Chancellor (1968, 1974) was unable to prevent the establishment of a dominance system amongst shoots on rhizome fragments of *Agropyron repens* by supplying potassium nitrate substantiating the argument that competition for nitrogen cannot be the only mechanism for dominance.

Apical dominance has several consequences and implications for the growth and survival of rhizomatous plants in the face of cultivations and

weed control procedures on arable land. Firstly, apical dominance allows the efficient deployment of resources for maximum horizontal spread of these plants. The production and retention of many dormant buds along with food reserves gives the rhizomatous plant a considerable potential for regeneration. Thus the prevention of rhizome growth must be of high priority in control measures for these plants. However, not only can a considerable regenerative capacity be built up during undisturbed growth, but also, regenerative capacity has been shown to be conserved when rhizomes are disturbed, for example during ploughing or other cultivation. Upon fragmentation, most of the buds on the rhizomes of *Agropyron repens* begin growth, but a new dominance system is soon established amongst the developing shoots, resulting in the continued suppression of a proportion of the buds (Chancellor, 1974; 1968, Leaky, Chancellor and Vince-Prue, 1978 a; 1978 b; McIntyre, 1972), with a minority growing on to form new aerial shoots. Re-imposition of apical dominance upon fragmentation has also been demonstrated in the rhizomes of *Sorghum halepense* (Hull, 1970). Chancellor (1968) and Hakansson (1968 a) have shown that re-inhibited shoots on cut fragments of *Agropyron repens* rhizomes are capable of further growth upon subsequent fragmentation. The re-imposition of dominance is undoubtedly a major factor in the survival of rhizomatous weeds on arable land. This phenomenon suggests that a minimum of cultivation is unlikely to destroy a rhizomatous weed population and indeed, may even assist its spread by enabling the establishment of new plants. The alternate destruction and stimulation of shoot growth and hence depletion of bud and food reserves is the basis of multiple-cultivation techniques advocated by Fail (1956) for the control of rhizomatous weeds.

A further consequence of apical dominance is that lateral buds are metabolically inactive and are therefore less likely to accumulate lethal levels of herbicides than are active buds (Sagar, 1960). Some interest has thus been shown in a search for chemicals which may release buds from apical dominance, rendering them both more able to import herbicides and more susceptible to cultivations (Chancellor, 1970; Chancellor and Leaky, 1972).

The subterranean vegetative organs of perennial weeds inhabiting

arable land are periodically subjected to various amounts of disturbance. Such disruption may result from the normal cultivation procedures in seed bed preparation, or may be part of a planned programme of cultural control of the weed as in the techniques of reserve exhaustion (Fail, 1956). During these cultivation procedures, the roots or rhizomes of the plants are cut to various lengths and displaced within the soil to various depths, depending predominantly upon the implement employed. Thus in order to understand the consequences of soil cultivation on perennial weeds, and with the hope of being able to devise more efficient weed control procedures, several authors have carried out experiments to quantify the effect of breakage and depth of burial of vegetative progagules.

When rhizomes of *Agropyron repens* are cut into fragments of various lengths, it is found that a greater percentage of the previously dormant buds produce shoots on shorter, rather than on longer fragments (Hakansson, 1968 a; 1971; Hakansson and Wallgren, 1976; Vengris, 1962). This phenomenon would appear to be the result of stronger correlative inhibition in longer fragments. If only a minority of buds on cut pieces of rhizomes actually form dominant shoots as suggested by Chancellor (1974), then it is axiomatic that a greater proportion will remain inhibited as the fragment length, and hence bud number per fragment increases. This effect of fragment length is not restricted to rhizomes. Hamdoun (1972) found that more adventitious buds and shoots were formed on a fixed total length of root of *Cirsium arvense* as it was divided up into smaller pieces. Similarly, in most cases, more aerial shoots developed per unit length, from shorter than from longer root pieces in *Sonchus arvensis* (Hakkansson and Wallgren, 1972). It would therefore seem that a correlative mechanism is also involved in determining the pattern of bud formation on severed roots of some species.

Correlative effects may be considerably more or less pronounced in different species. For example, the data of Hakansson and Wallgren (1976) showed that over a range of fragment length and burial depth, a greater proportion of rhizome buds grew to produce shoots in *Agropyron repens* than in both *Holcus mollis* and *Agrostis gigantea*.

The practical implication of the variable degree of re-instatement

of correlative inhibition with variation in the length of root and rhizome fragments is that in a multiple cultivation technique designed to exhaust buds and food reserves, the smaller the propagules are, the more rapidly will the desired result be achieved. This has not however, been demonstrated in a field situation.

Species vary considerably with regard to the depth from which they may regenerate. For example, Coupland, Selleck and Alex (1955) found that shoots of *Euphorbia esula* could emerge from the soil from undisturbed roots at a depth of 42.5 cm. It was also shown that stands of this plant, buried under 90 cm of soil produced emerged shoots within one year of burial. Other examples of the depths from which shoot emergence can occur are; *Cirsium arvense*, at least 50 cm (Hamdoun, 1972); *Agropyron repens*, at least 30 cm (Hakansson, 1968 b); *Holcus mollis* and *Agrostis gigantea*, at least 16 cm (Hakansson, 1971) and *Sonchus arvensis*, at least 30 cm (Hakansson, 1972). The depth at which rhizome and root fragments are placed in the soil profoundly affects their ability to establish emerged shoots and hence new plants. When rhizome fragments of *Agropyron repens* were planted on the soil surface, shoot production was low and erratic and there was a high rate of mortality (Hakansson, 1968 b). As planting depth increased, an optimum depth for regeneration was passed through (2.5 to 5.0 cm) and below this, the rate of shoot emergence declined. As a consequence of the effect of fragment length on the degree of re-establishment of correlative inhibition, longer rhizome fragments of *Agropyron repens* more readily form emerged shoots than do shorter fragments (Hakansson, 1968 b; 1971; Vengris, 1962). Because longer fragments have a smaller proportion of activated buds, the shoots which are produced have a larger supply of food reserves and thus have a greater capacity for emergence from depths at which shoots from shorter fragments fail. As a result of this interaction between rhizome fragment length and depth of burial, Hakansson (1968 b) was able to estimate the LD 50 depth of fragments. He showed that the depth at which 50% of rhizome fragments of *Agropyron repens* died without producing a shoot above the surface (log. scale) increased in proportion to the increase in dry weight or length (log. scale) of planted pieces.

The effect of competing crops in relation to the effects of depth of placement and rhizome fragment length has been studied by Hakansson

(1968 a; b). It was found that competition from a white mustard (*Sinapis alba*) checked the weight production of plants from smaller rhizome pieces more than from longer pieces, and also reduced production of the plants from pieces planted at 10 cm more than from those at 5 cm depth. These effects were the result of shoots from smaller fragments being of lower vigour than those from longer fragments (Hakansson, 1968 b), and those from deeper placement having a slower rate of emergence thus putting them at a disadvantage with the mustard. It was concluded that in practice, a crop has a better chance of suppressing a stand of *Agropyron repens* the deeper the rhizomes have been buried and the more they have been disjointed in preceeding soil operations. This general principle has been outlined by Hakansson (1971).

The maximum depth to which plants may penetrate the soil is an important factor to be considered when devising control measures for plants which can regenerate from roots and rhizomes because the effect of cultivation and herbicides will depend on the extent to which propagating and food storage tissue remains below cultivation and herbicide depth. Depth of penetration may be quite shallow as in the case of *Agropyron repens* which will sometimes form rhizomes in the top few centimetres of surface litter (Palmer and Sagar, 1963). However more commonly the rhizomes of this species occur down to 10 to 15 cm (Hakansson, 1968 b) and may occasionally reach 40 cm in alluvial soils (Palmer and Sagar, 1963). Coupland and Alex (1955) found that the roots of *Euphorbia esula* penetrated to a maximum depth of 2.45 m in a wide range of soils and few plants of this species reached down to less than 1.2 m.

When a fragmented root or rhizome system begins to regenerate, there is inevitably an initial loss in the total dry matter of the propagule because assimilation is absent until the shoots emerge and photosynthesis begins. In *Agropyron repens* it was demonstrated that regardless of fragment length, depth, and time of planting, the propagules reached a minimum dry weight when the emerged shoots had formed from three to four leaves, and coinciding with this minimum were minima in water soluble carbohydrates and nitrogen content of the planted rhizome fragments (Hakansson, 1967). Immediately after the minimum in dry weight, new rhizomes and tillers were formed and a rapid increase in total weight began. The developing plants were most susceptible to re-burial at the

dry weight minimum, presumably because the remaining rhizome buds and buds on the primary vertical shoots would have had a reduced food reserve from which to draw upon and also, as new rhizomes had not yet been formed, the potential regrowth would have been very low in comparison to that after new rhizomes had been initiated. It was noticed that after the dry weight minimum had been passed, the rhizome pieces increased in weight and were replenished with carbohydrate and nitrogen. *Sonchus arvensis* was shown to proceed through a similar pattern of early regenerative growth, exhibiting dry weight minima just prior to the formation of new reproductive roots, at which time the plants had produced five to seven leaves and were most susceptible to re-burial (Hakansson, 1969). It was argued therefore, that when repeated soil cultivations are to be used in the control of these plants, with the intention eradicating the stand with the lowest number of operations, the first operation should be carried out as soon as practicable, and cultivation should not be repeated until the whole stand has just passed its dry-matter minimum (Hakansson, 1967; 1969). This critical stage of development could be recognised in *Agropyron repens* when the regrowing shoots had about three to four leaves and in *Sonchus arvensis* when five to seven leaves had been produced.

The observation that the rhizomatous nature of yarrow is apparently important for the survival of the species on cultivated soils prompted the investigations reported in this section. The main objectives were:

1. To determine if plants developing from both seeds and rhizomes were able to form new rhizomes in their first season of growth and to record the pattern of axillary bud development on the rhizomes of undisturbed plants.

2. To define the regenerative responses of rhizomes after fragmentation and burial to various depths in the soil.

3. To determine if there was any seasonality of bud activity on single-node rhizome fragments.

4. To establish the pattern of development of plants regenerating from rhizome pieces planted in the summer and autumn in order to define the stage at which new rhizomes are formed.

5.2 EXPERIMENT 1. RHIZOME FORMATION AND THE PATTERN OF BUD DEVELOPMENT.

5.2.1 Materials and Methods

In the summer of 1976 an outdoor pot experiment was set up to allow a comparison of the morphogenesis of yarrow plants from seed and rhizome fragments. A shading treatment was incorporated in this preliminary experiment with the intention of providing a basis for further research into developmental patterns and the effect of shading (Chapter 3). The results presented here pertain only to the development of rhizomes in full daylight.

Ten-leaf seedlings germinated on 16 November 1976, and unsprouted single-node rhizome cuttings measuring 2 cm in length and with the bud centrally placed, were transplanted into black polythene planter bags measuring 30 x 30 x 60 cm deep, on 25 December 1976. The rhizome cuttings were placed one cm beneath the soil surface. The bags were placed out in the open at an experimental site at Lincoln College. Each bag contained approximately 18 litres of firmly packed Wakanui silt loam which had been sterilised with methyl bromide gas to ensure adequate weed control during the experiment. The rhizome sections were obtained from material dug from a field population near Rolleston, Canterbury, several days before planting. The seeds used had been collected from a road-side population in Christchurch in March 1976.

The plants were regularly watered so that the soil was always moist and water did not become limiting for growth. On six occasions; 23 Jan, 11 Feb., 26 Feb., 27 March, 17 April and 19 June, 12 plants of each propagule type were randomly selected and washed from their containers. The plants were then dissected into rhizomes, and other components not considered here, and counts were made of the number of primary rhizomes, dormant and active axillary buds, and the total length of rhizome.

Seed-propagated plants were initially older and larger than the rhizome-propagated plants and flowered profusely in comparison to the latter. It was therefore considered hazardous to attempt a critical comparison of rhizome formation and development between plants of the two propagule types, and accordingly statistical comparisons were not made.

However standard deviations of the 12-plant samples were calculated to indicate the variability of the plants.

5.2.2 Results

The means and standard deviations from which the Figures in this section were constructed are given in Appendix XXVII. It can be seen in Figure 5.1 that both seed and rhizome-propagated plants produced rhizomes in the first season of growth, and apparently initiated rhizomes at a similar rate. The rate of initiation of rhizomes was nearly constant throughout the experimental period in both types of plants, and showed little sign of declining with the onset of winter in June. It will be noticed that the standard deviations shown in Figure 5.1 (and in all other Figures of Expt. 1) are considerably higher for the seed-propaged plants; an indication of greater genetic variability amongst the seeds than the rhizome fragments. Indeed, it is likely that the rhizome fragments were of the same genetic constitution because they were derived from rhizomes collected from a very small area. By early winter (June) both types of plants had formed approximately 80 primary rhizomes.

As rhizome initiation was occurring, considerable rhizome elongation was also taking place (Fig. 5.2). Total length of rhizome increased throughout the period of observation and the rate of increase tended to rise with time probably as a consequence of the increasing numbers of rhizomes. The rate of total length increase was slower in seed-propagated plants in March and April which may be explained by greater competition for assimilates between the rhizomes and the aerial parts in these plants as a consequence of the more profuse flower stem production. Flowering was less vigorous in the rhizome-propagated plants possibly because of their smaller initial size and the late establishment of the trial as a whole. Later in the autumn and early winter, the rate of rhizome elongation was similar in plants of both propagule types, but as a consequence of the earlier differences in rates, seed propagated plants had produced considerably less total length of rhizome than had rhizome-propagated plants by late June (Fig. 5.2).

As rhizomes were elongating, nodes were produced at intervals of approximately 1.0 to 1.5 cm. Internode length varied and it was not uncommon, especially in the portion of rhizomes produced during the autumn

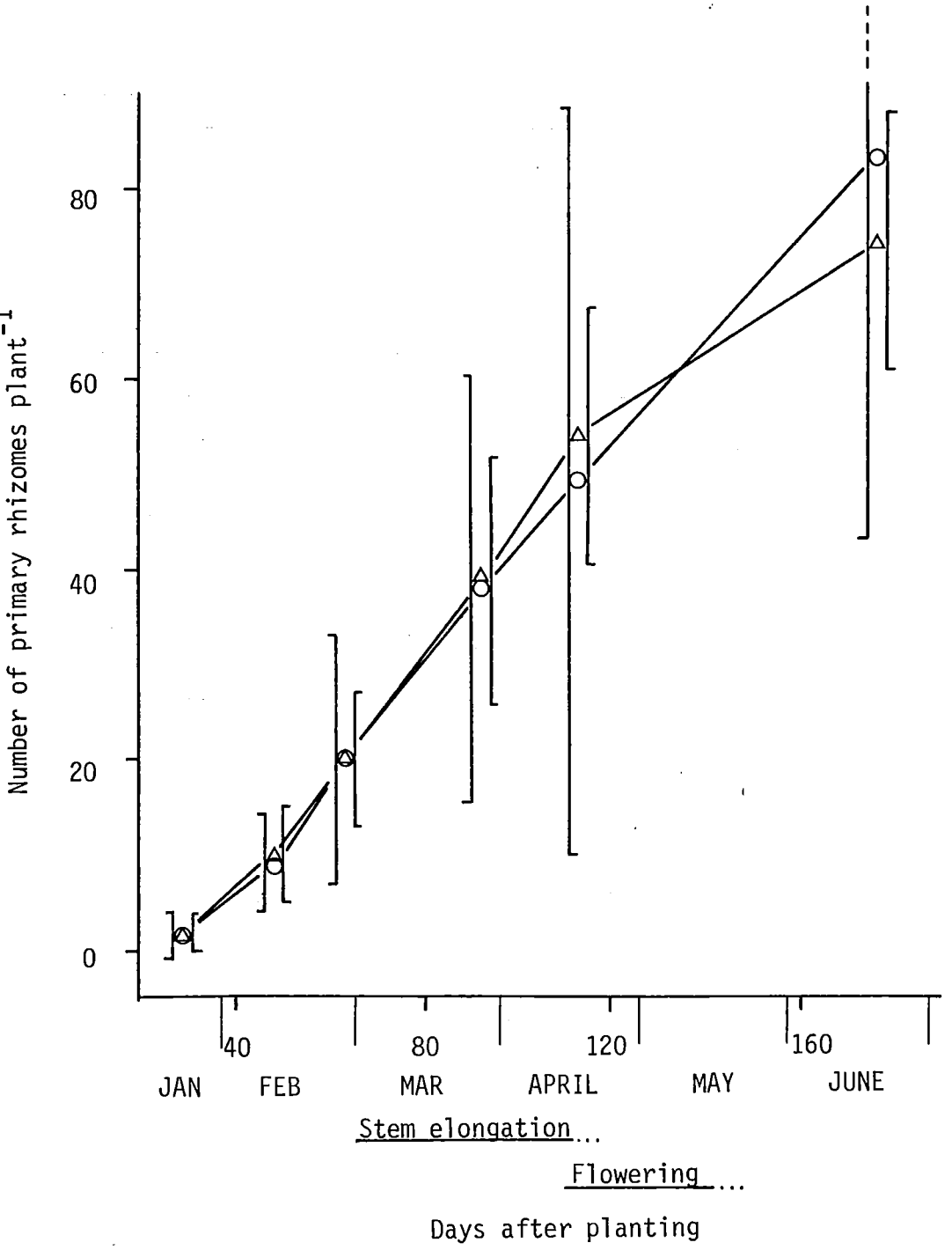


Figure 5.1 The increase in the numbers of primary rhizomes plant^{-1} from mid-summer until early winter, in plants propagated from seed and single-node rhizome fragments. Vertical bars are twice the sample standard deviation; points are means of 12 plants.

○——○, seed propagated; △——△, rhizome propagated.

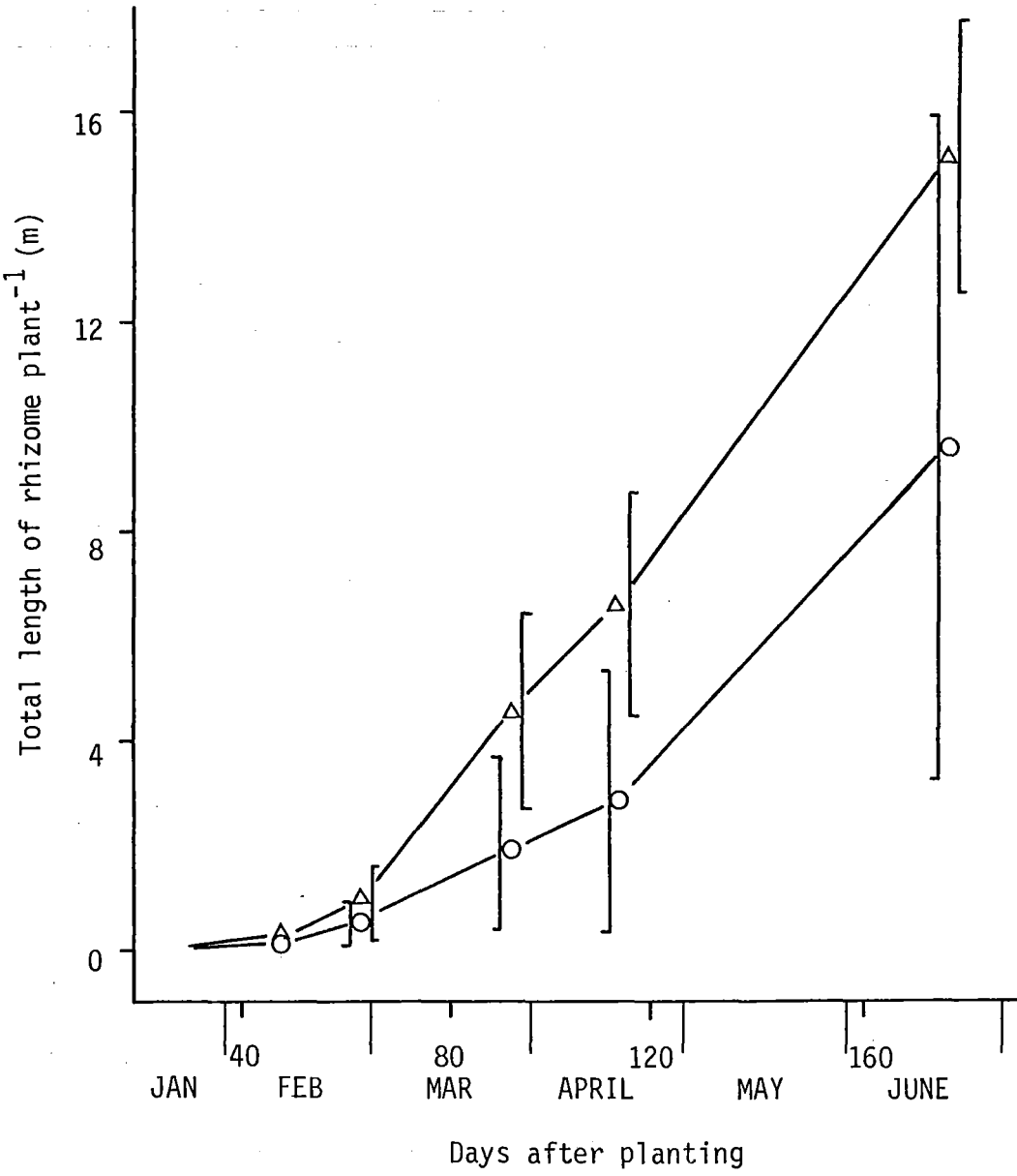


Figure 5.2 The increase in total length of rhizomes plant^{-1} from mid-summer until early winter in plants propagated from seed and single-node rhizome fragments. Bars are twice the sample standard deviations; points are means of 12 plants. O——O, seed propagated; Δ——Δ, rhizome propagated.

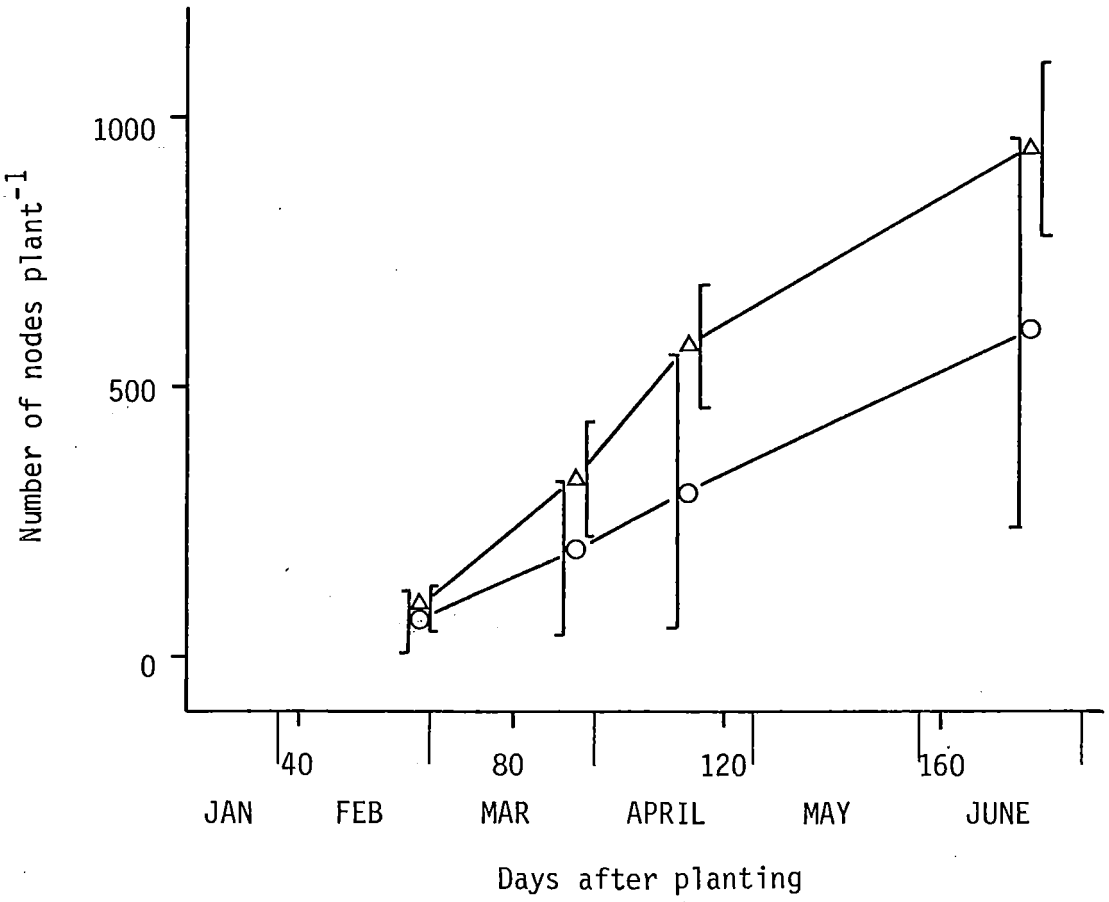


Figure 5.3 The increase in number of rhizome nodes plant^{-1} from mid-summer until early winter, in plants propagated from seed and single-node rhizome fragments. Bars are twice the sample standard deviations; points are means of 12 plants. O—— O, seed propagated; Δ—— Δ, rhizome propagated.

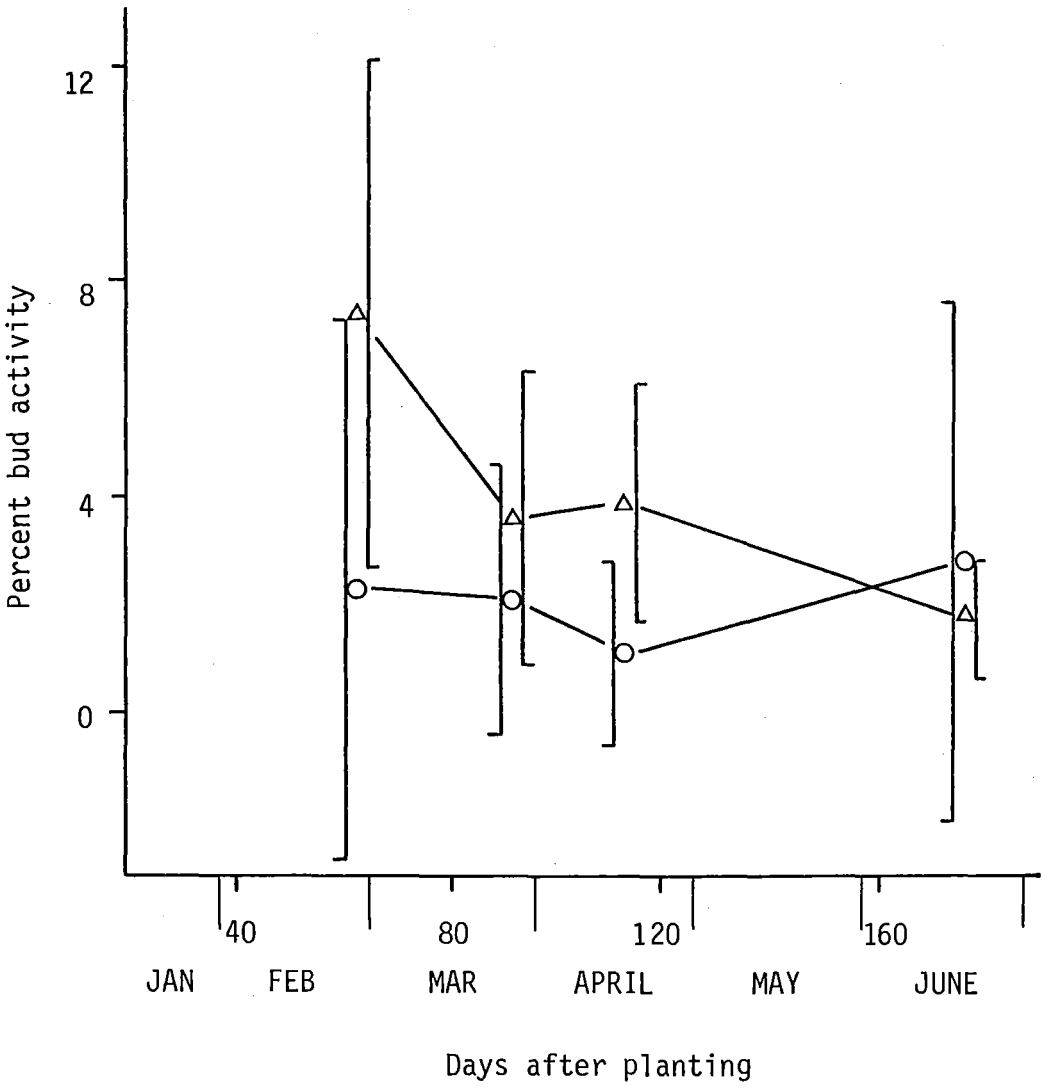


Figure 5.4 Percentage of axillary rhizome buds showing activity during the mid-summer to early winter period, in plants propagated from seed and single-node rhizome fragments. Bars are twice the sample standard deviations; points are means of 12 plants. O——O, seed propagated; Δ——Δ, rhizome propagated.

and winter, to find internodes up to 6.0 cm. On the other hand, internodes as short as 0.2 to 0.3 cm were frequent on the basal sections of rhizomes. By the time of the final sampling on 19 June, rhizome-propagated plants had formed 930 nodes while seed-propagated plants had produced 600, a reflection of the difference in elongation rate during March and April (Fig. 5.3).

At sampling dates beginning on 26 Feb., a count was made of the total numbers of sprouted axillary buds on primary rhizomes and was expressed as a percentage of the total number of primary axillary buds (Fig. 5.4). It can be seen that a very high degree of axillary bud inactivity was maintained on the rhizomes of both propagule types throughout the entire period. Although approximately 7% of the lateral buds on the rhizomes of rhizome-propagated plants had become active during late February, only one to 4% were active during the remainder of the period. Inactive buds showed no growth at all, measured approximately 1 to 2 mm in length, and remained in a healthy and viable state throughout.

During the course of this experiment it was noticed that axillary buds were activated under one of three circumstances. First, when the apex was damaged or broken off due to contact with the wall of the container or as a result of the chewing of soil inhabiting organisms, Greasy cutworms were found in some pots in which rhizome damage of the latter type had occurred (Fig. 5.5). Secondly, after the apical bud had emerged from the soil to form a new rosette (Fig. 5.6 b). This photograph (and Fig. 5.6 a) was of a field-grown plant, but illustrates clearly what was observed to occur in the container-grown plants. Rhizomes growing actively and unimpeded through the soil were rarely found to have actively growing axillary buds (Fig. 5.6 a). Thirdly, branching was also recorded in regions of rhizomes along which nodes had previously been formed very close together (see Fig. 2.6). This latter phenomenom usually occurred in the central regions of rhizomes and was possibly a result of physical impediment of the apex by localised areas of dried and hard soil. It was not commonly observed, and subsequent to the return of favourable conditions, internodes of normal length were again produced.

In all cases of bud activity, secondary rhizomes were produced and although these occasionally grew only a short distance before emerging as

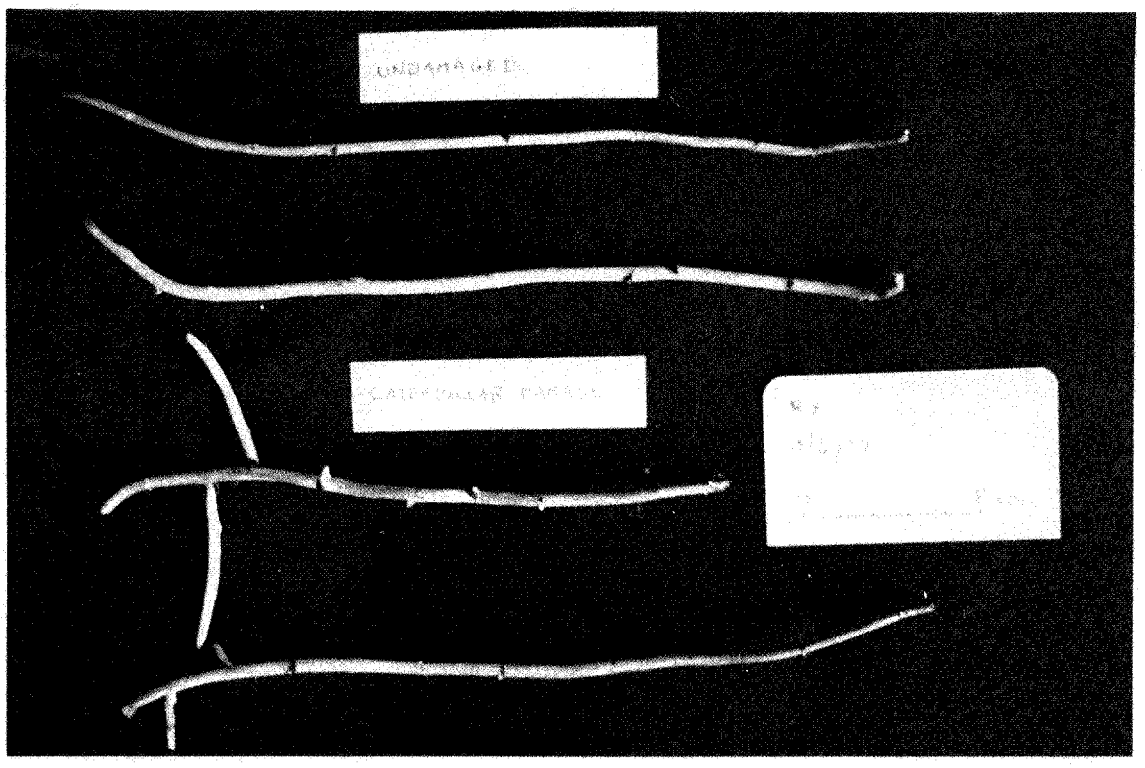


Figure 5.5 The effect of damage to the apical bud on the growth of axillary rhizome buds. All four rhizomes were attached to the parent plant, but the apices of the lower two had been damaged, probably by greasy cutworm caterpillars which were found in the pots. The apical regions are to the left of the photograph.

a)

b)

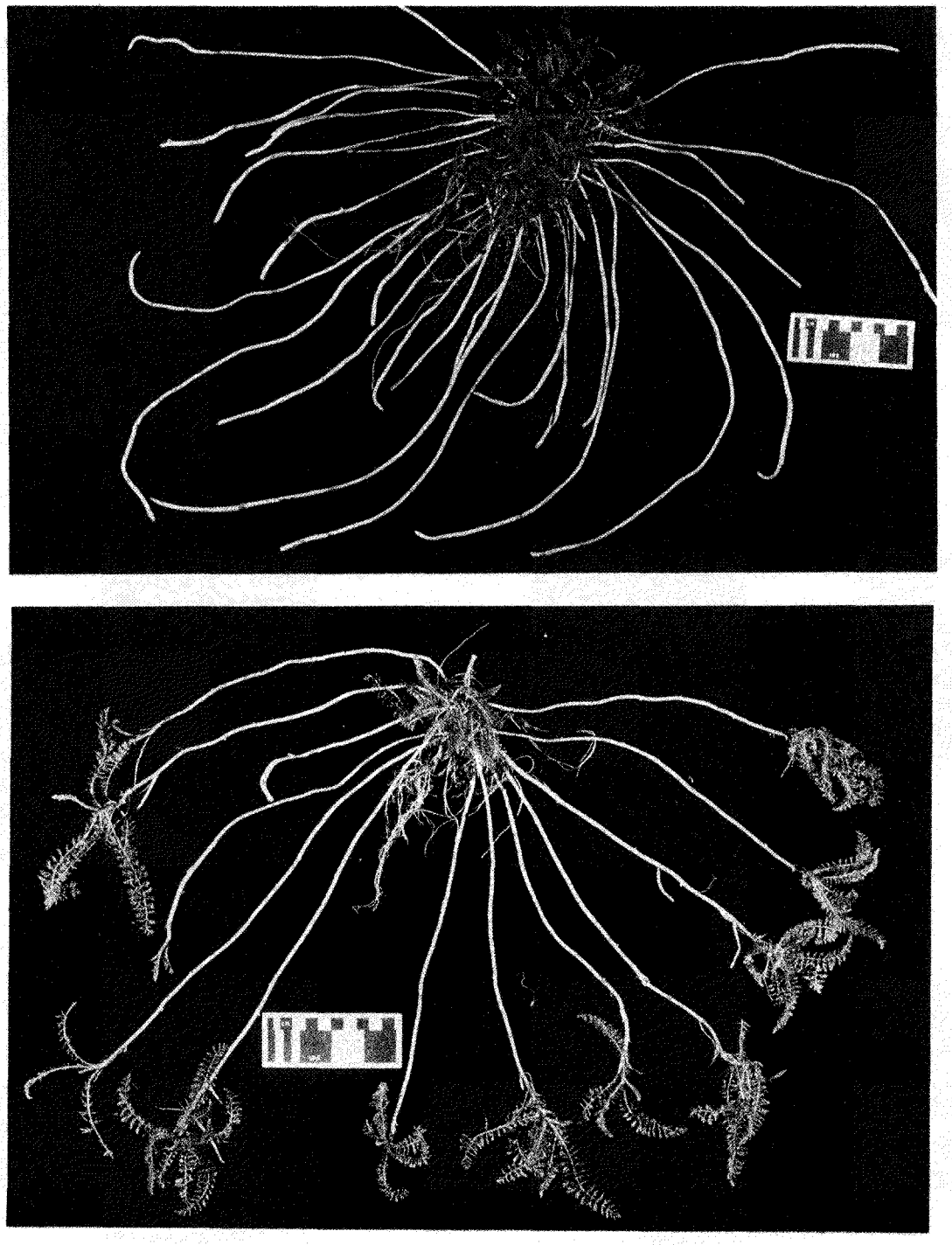


Figure 5.6 Apical dominance in the rhizome system of plants grown in a cultivation field.

a) A high degree of axillary bud inactivity is evident in this plant collected during the winter of 1978.

b) Buds near the emerged rhizome apices in the spring of 1978 have become active and are forming new rhizomes.

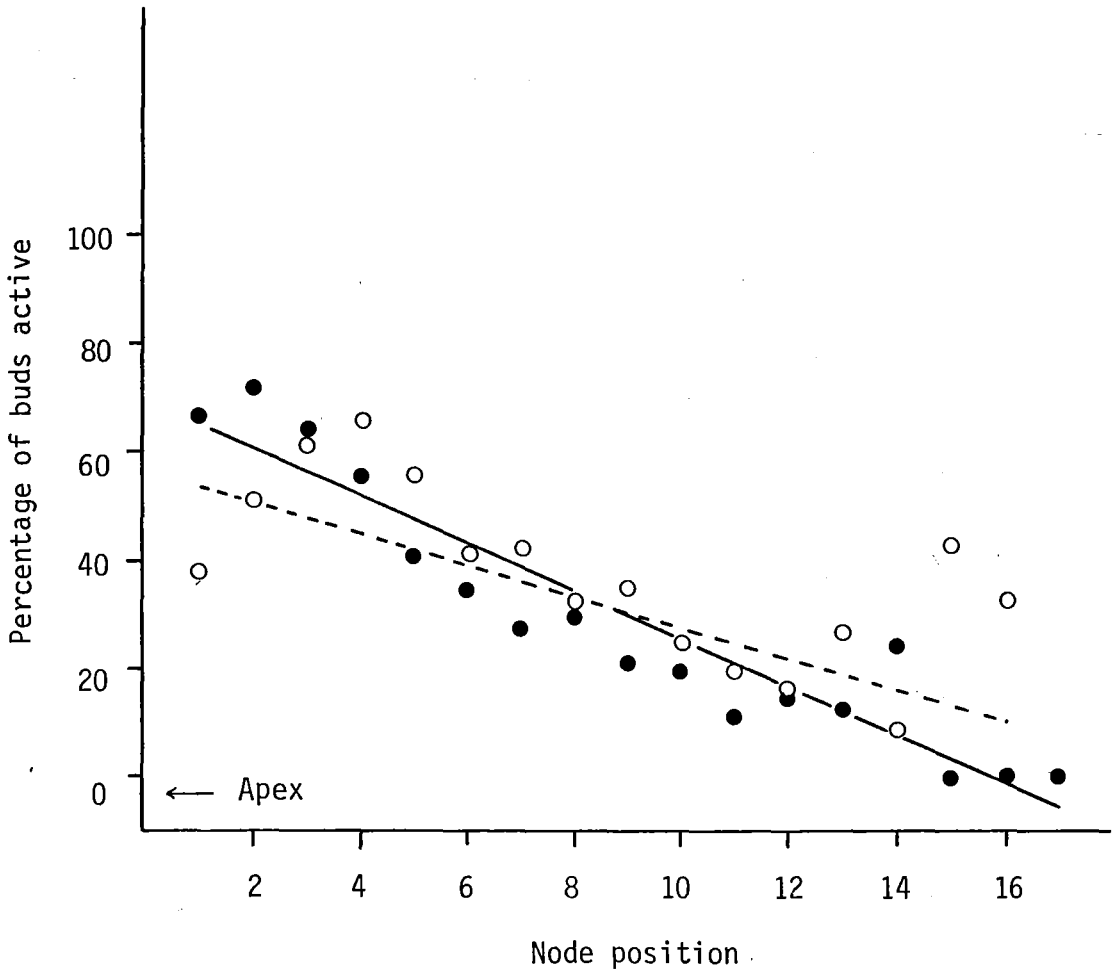


Figure 5.7 Polarity of axillary rhizome-bud activity. ----o, rhizome-propagated plants, $y = 56.8 - 2.3x$, $r = -.67^{**}$; ——●, seed-propagated plants, $y = 69.6 - 4.4x$, $r = -.94^{**}$. The number of rhizomes (buds) per sample for rhizome-propagated plants, from node 1 to node 16 inclusive were; 72, 72, 72, 72, 71, 71, 65, 57, 49, 44, 35, 24, 15, 6, 4, 2. Similarly, for seed-propagated plants, the number of buds per sample from node 1 to node 17 were; 55, 55, 55, 55, 55, 52, 46, 40, 35, 26, 20, 12, 10, 5, 1, 1, 1, 1.

leafy aerial shoots, axillary buds were not observed to form directly into aerial shoots when sprouting on intact rhizomes attached to the parent plant. The secondary rhizomes grew horizontally and maintained a high degree of bud inactivity until possibly they experienced one of the three phenomenon just described.

Under the circumstances of one and two above, there was an obvious sequence of bud activity. At the final harvest (19 June), all rhizomes from the 12 plants of each propagule type, with emerged apices, were assessed for presence or absence of branching at all nodes from the first node back from the lowest bearing an aerial leaf. The data from all rhizomes was bulked and is presented in Figure 5.7 as the percentage of emerged rhizomes with active buds at each of the nodal positions. There was a clear trend toward increasing activity approaching the apical end of the rhizomes of plants from both propagule types.

5.3 EXPERIMENT 2. THE EFFECT OF FRAGMENTATION AND BURIAL OF RHIZOMES ON REGENERATIVE CAPACITY.

5.3.1 Materials and Methods

A field trial was initiated on a Wakanui silt loam with the objective of investigating the effect of fragmentation and depth of burial of rhizomes on the production of new shoots. The experiment was designed as a randomised, complete block with three fragment lengths (4, 8 and 16 cm), six depths of burial (on the surface, 2.5, 5.0, 10.0, 20.0 and 30.0 cm), and six replicates.

Rhizomes for this experiment were forked on 21 November 1978 from a population established during the summer of 1977 on a Wakanui silt loam. The plants had grown undisturbed and by the time of collection, rhizomes of sufficient length, with inactive axillary buds were available. After forking from the soil, intact rhizomes were severed from the parent plants and taken to the laboratory in dampened calico sacks to prevent desiccation. They were immediately placed in trays and kept at $5^{o}C$ in a refrigerator to prevent premature bud activity. Rhizomes were taken from the refrigerator in small groups at a time, cut to the required lengths and quickly replaced in the damp calico and returned to the refrigerator. The appropriate lengths of rhizome were obtained with the aid of cutting tools which consisted of a metal frame with a razor blade attached to each

end. These devices (one for each fragment length) were pressed down into the rhizome from which a section was required. The rhizomes were placed on a piece of rubber to prevent blunting the blades and to provide some cushioning which assisted cutting. To prevent the possibility of including immature apical or moribund and/or closely spaced basal buds, the sections were obtained from the middle regions of the rhizomes. Rhizomes with damaged or sprouted buds were avoided. The procedure gave sections of constant length, with similar numbers of buds. The mean bud number and dry weights of the prepared sections were estimated from a random sample of 30 pieces and are given in Table 5.1

Table 5.1 Characteristics of the planted rhizome sections, based on a random sample of 30 sections. Sample standard deviation in parentheses.

length of section (cm)	dry weight section^{-1} (g)	node number section^{-1}
4	.081 (.049)	1.3 (.45)
8	.188 (.057)	2.8 (.81)
16	.339 (.126)	4.7 (.76)

The rhizome sections were planted on 29 November 1978. For each planting depth, 10 rhizome sections of a particular length were placed on the bottom of small trenches measuring 20 x 60 cm, and arranged parallel to each other 6 cm apart. The trenches were arranged in six adjacent rows of 18, each row constituting one replicate. The 18 treatment combinations were allocated at random to the 18 treatment units within each replicate. Immediately after placement of the rhizome sections, which had been kept moist during planting, the trenches were filled with a Wakanui silt loam which had been sterilised with methyl bromide to destroy weed seeds and rhizomes of *Agropyron repens*. The soil was packed firmly into the trenches to avoid later compaction and alteration of the depth of the fragments. Emerged weeds in the surrounding soil were controlled with glyphosate applied from a knapsack sprayer, and the entire experiment was overhead-irrigated on 4 December to ensure sufficient moisture for bud sprouting and initial growth.

The experiment was harvested on 12 March 1979, 103 days after planting, and all plant material was recovered, including the original planted rhizome fragments, unless these had decayed away. Each sample was washed free of adhering soil and divided into two parts according to whether the original rhizomes had decayed away or remained viable. The numbers of emerged and unemerged shoots were counted and the fractions; original rhizome, new rhizome, subterranean vertical shoots, tops, roots and dead material were separated, dried, and weighed.

5.3.2 Results

The means from which the Figures in this section were constructed are given in Appendix XXVIII. The percentages of planted rhizomes which survived are presented in Figure 5.8 a. Rhizome sections were considered to have survived if they had remained partly or wholly undecayed and produced at least one emerged shoot. Most sections considered to have survived showed little sign of decay. Although a few sections decayed back to the shoot nearest the end of the section, only a minority of buds appeared to have been lost in this way. Those sections which failed to survive had mostly decayed away and often could not be found and for those which were found, it was not always possible to determine if shoots had begun to grow and failed to reach the surface, or whether there had been no shoot growth at all.

There was no rhizome survival from surface plantings or from depths greater than 10 cm but 100% of the fragments survived at 2.5 cm (Fig. 5.8 a). At 5.0 and 10.0 cm depth, survival declined with increasing burial depth and decreasing fragment length.

The number of emerged shoots expressed as a percentage of the total number of planted buds showed the regenerative capacity of the bud population declined with increasing depth of burial below 2.5 cm (Fig. 5.8 b). No aerial shoots were formed from surface-planted pieces or from those at 20 and 30 cm. Aerial shoot number as a percentage of planted buds tended to increase with increasing fragment length at a depth of 10 cm but tended to decline at shallower depths.

The activity of axillary buds on undecayed rhizome sections is presented in Figure 5.9. These values are the number of buds which had become active, regardless of whether they had formed emerged shoots, expressed

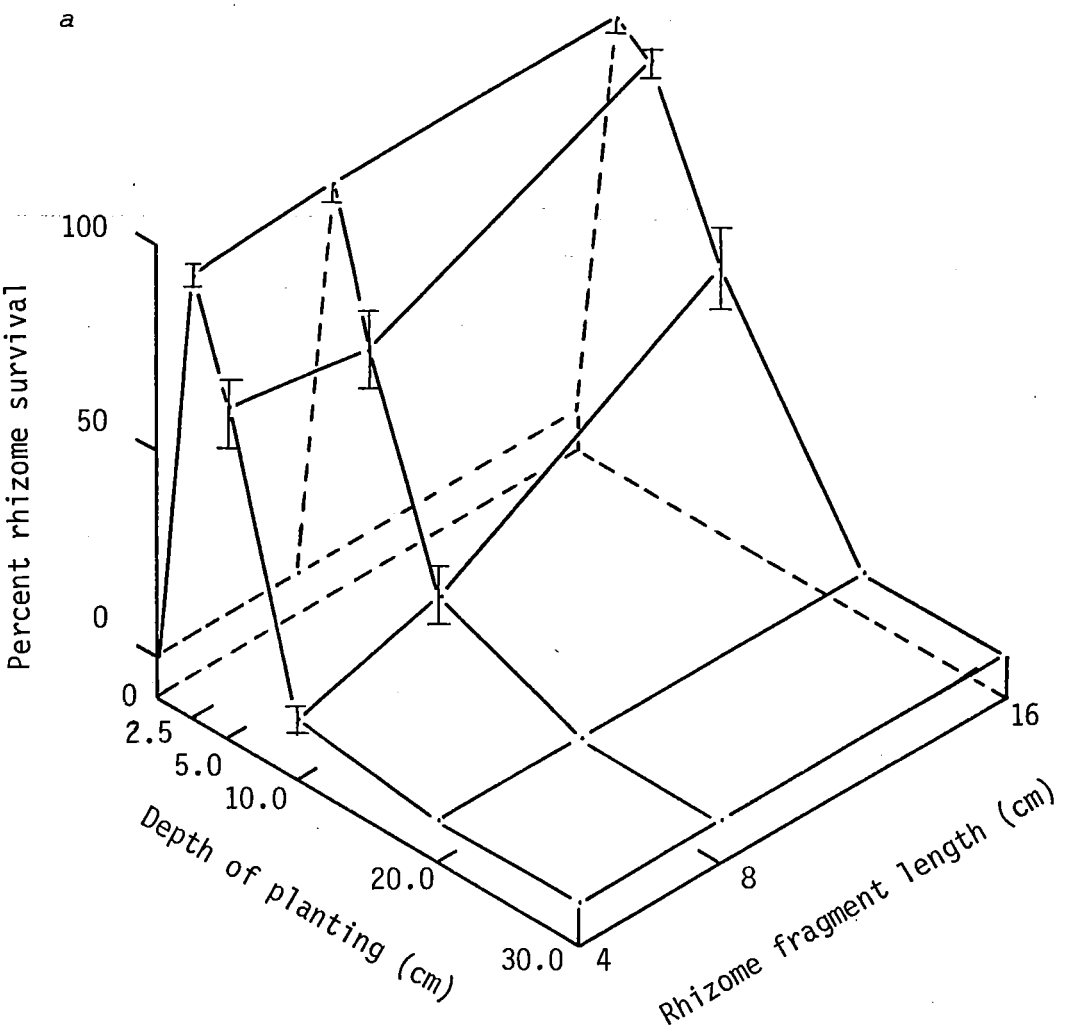


Figure 5.8 See page 196.

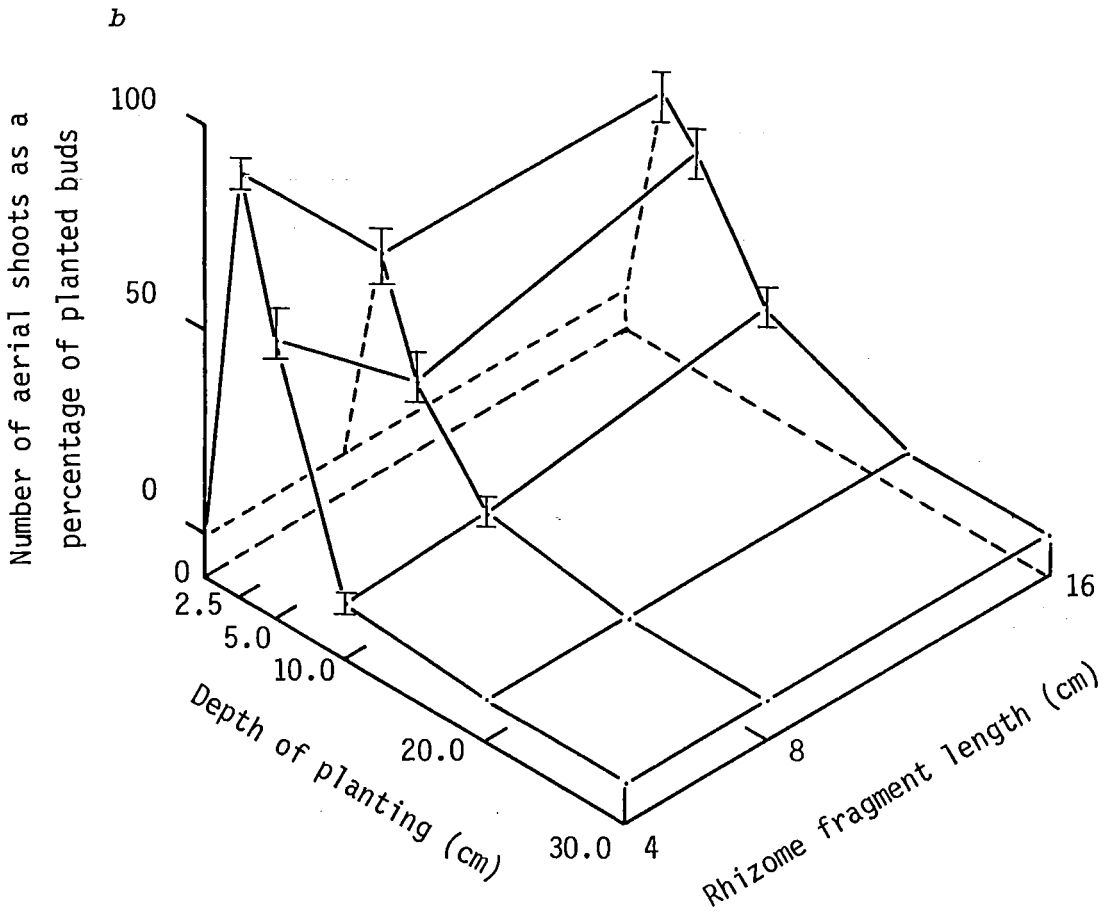


Figure 5.8 The effect of length and burial depth of rhizome fragments on their survival and aerial shoot production. Bars are twice the standard errors of the means; points are means of six replicates.

a percentage of fragments which remained partly or wholly undecayed with at least one aerial shoot.

b number of aerial shoots as a percentage of number of planted buds.

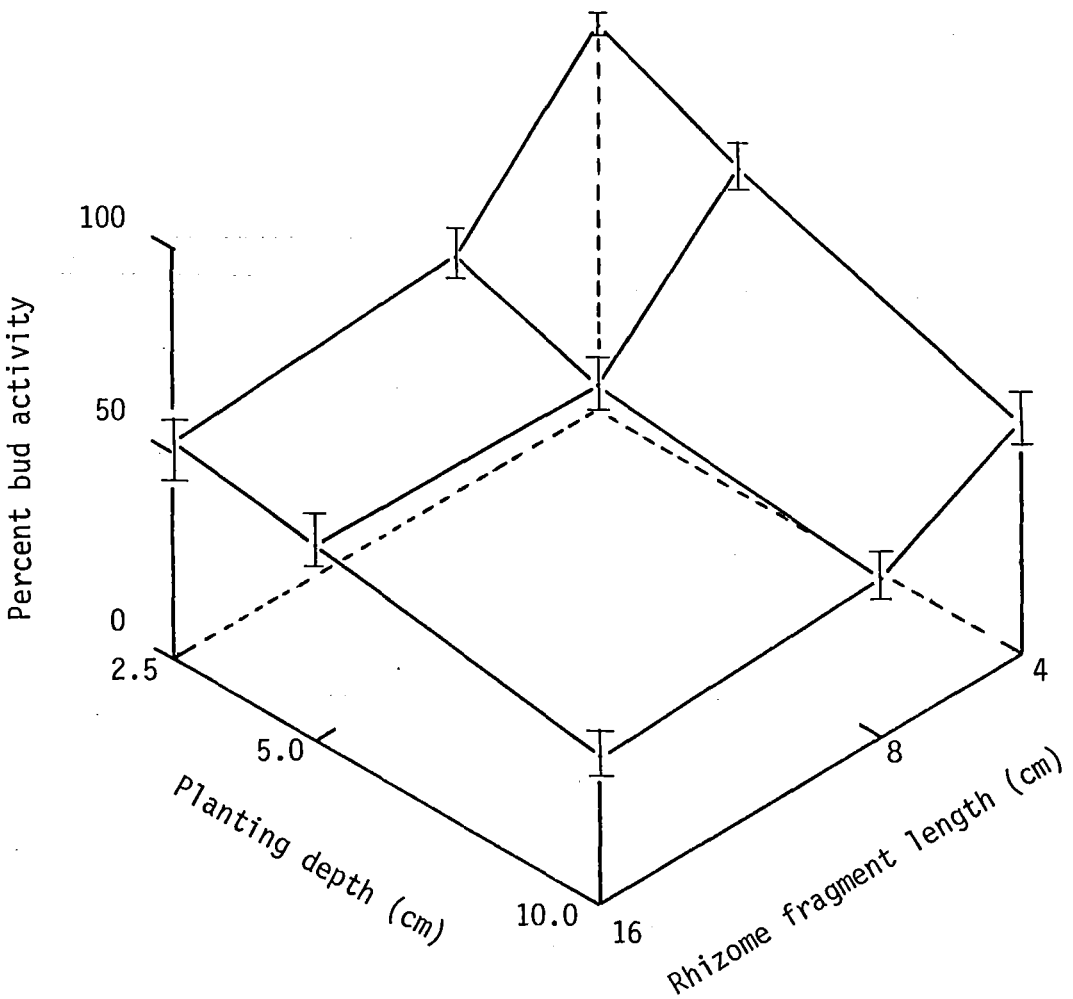


Figure 5.9 The effect of length and burial depth of rhizome fragments on the percentage of axillary buds which became active on fragments remaining partly or wholly undecayed after 103 days of burial. Bars are twice the standard errors of the means; points are means of 6 replicates.

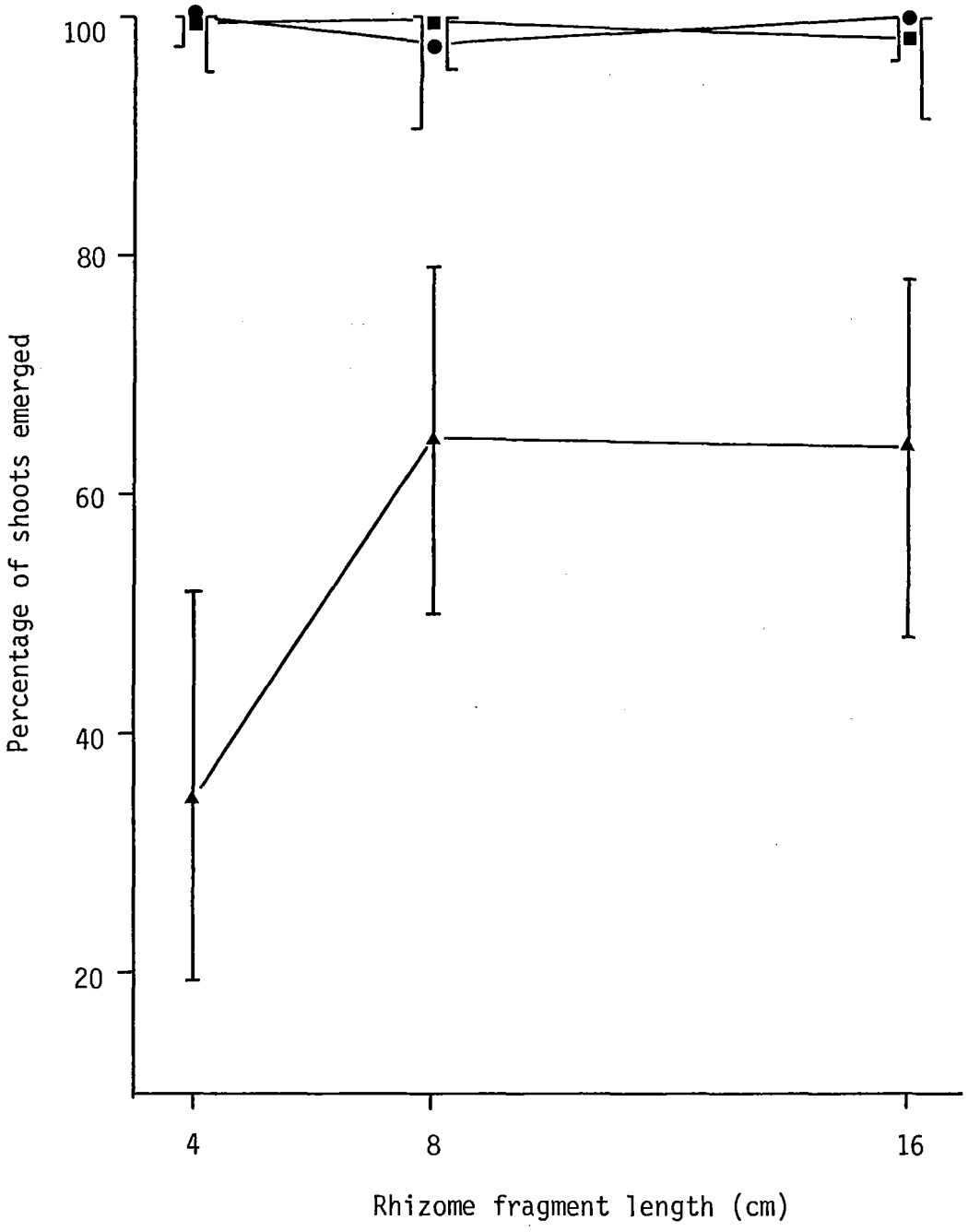


Figure 5.10 The effect of length and burial depth of rhizome fragments on the percentage of active axillary buds which had formed emerged shoots after 103 days of burial. Bars are twice the standard errors of the means; points are means of 6 replicates. ● —— ●, ■ —— ■, ▲ —— ▲, represent burial depths of 2.5, 5.0 and 10.0 cm respectively.

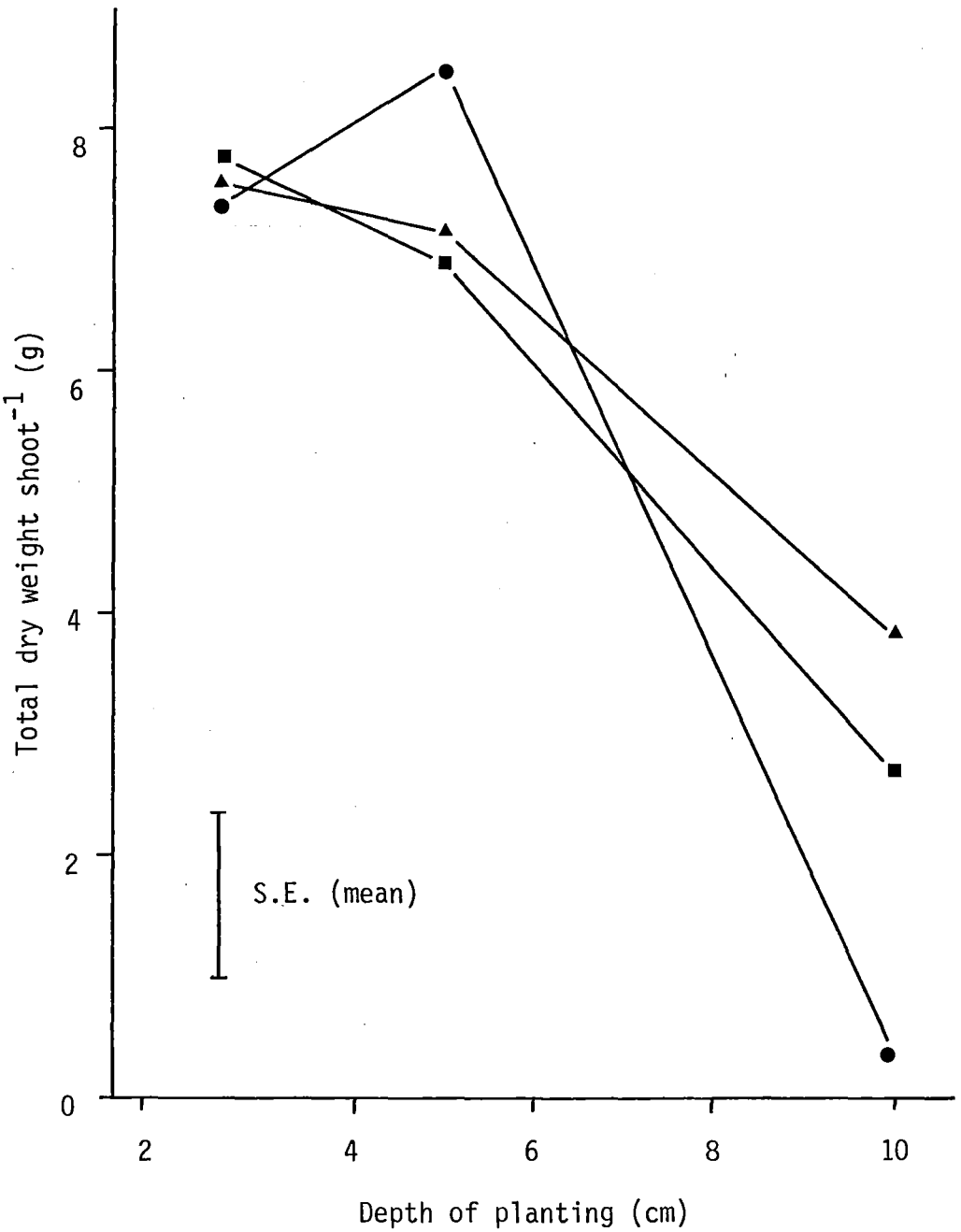


Figure 5.11 The effect of length and burial depth of rhizome fragments on the total dry weight emerged shoot^{-1} after 103 days of burial. Points are means of 6 replicates. ●——●, ■——■, ▲——▲, represent 4, 8 and 16 cm lengths of rhizome respectively.

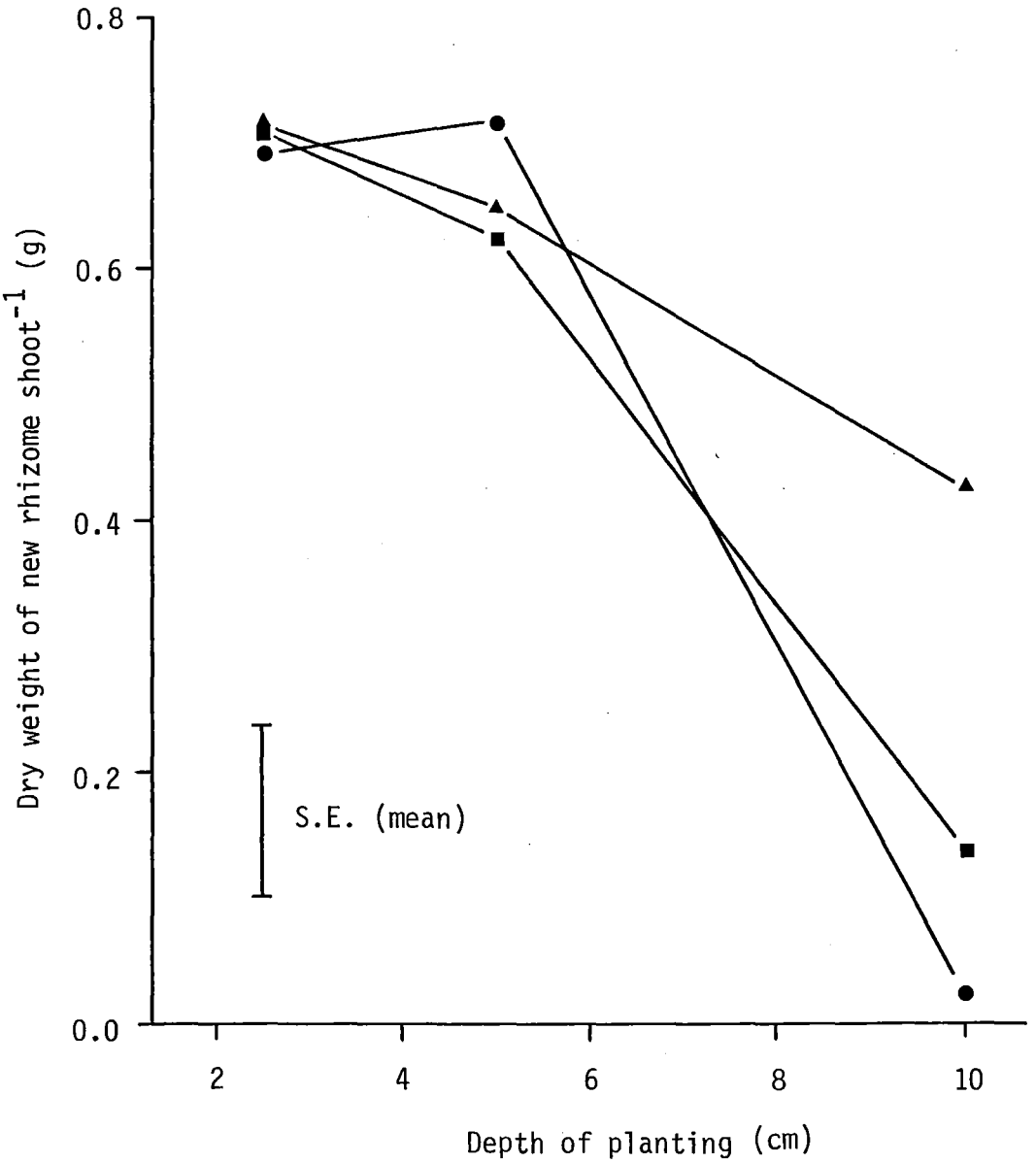


Figure 5.12 The effect of length and burial depth of rhizome fragments on the dry weight of new rhizome shoot^{-1} after 103 days of burial. Points are means of 6 replicates. ● —— ●, ■ —— ■, ▲ —— ▲, represent 4, 8 and 16 cm lengths of rhizome respectively.

as a percentage of the mean number of buds which had been available on the undecayed sections. It can be seen that bud activity declined with increased depth of planting and with increase in fragment length, most markedly from 4 to 8 cm. Nearly 100% of the activated buds at depths of 2.5 and 5 cm formed emerged shoots (Fig. 5.10) but at 10 cm depth, 65% of the activated buds emerged from 8 and 16 cm fragments and only 35% from 4 cm fragments.

In order to assess the vigour of the regenerated plants produced by the end of the experiment (103 days of burial), the total dry weights and rhizome dry weights shoot^{-1} were calculated (Figs. 5.11; 5.12). Shoot vigour generally declined slightly with an increase in depth from 2.5 to 5.0 cm but declined markedly at 10.0 cm depth. Shoot vigour at 10.0 cm depth declined with decreasing fragment length (Figs. 5.11; 5.12) and it can be seen from Table 5.2 that this decline in vigour as measured by dry weight was associated with a decrease in flower stem formation. There were no stems produced by plants formed from shoots emerging from 4 cm fragments planted at a depth of 10 cm.

Table 5.2 The effect of length and depth of burial of rhizome fragments on the formation of flower stems. Values are the percentage of plots with flower stems present on 12 March 1979.

	fragment length (cm)		
burial depth (cm)	4	8	16
2.5	100	100	100
5.0	67	100	100
10.0	0	33	67

5.4 EXPERIMENT 3. SEASONALITY OF BUD ACTIVITY AND SHOOT VIGOUR OF SINGLE-NODE RHIZOME FRAGMENTS

5.4.1 Material and Methods

The seasonality of rhizome-bud activity was studied in an established stand of yarrow growing on a Wakanui silt loam soil on the Lincoln College Research Farm from 13 October 1977 until 27 April 1978 (Site 1). The experiment was a randomised complete block design, incorporating seven

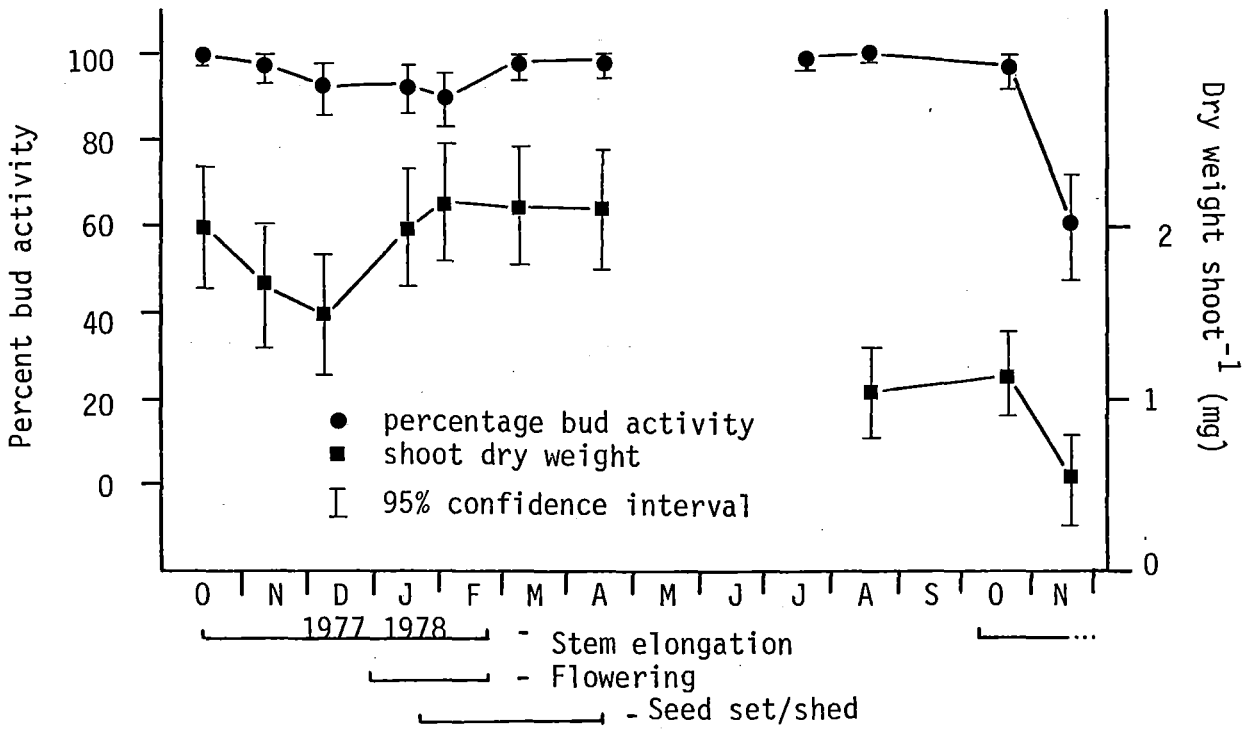


Figure 5.13 Percent bud activity and shoot dry weights of single-node rhizome fragments. (See Appendix XXIX).

sampling dates which were provided for with small plots measuring 1.0 x 1.0 m, and four replicates. The study was continued in the same layout in another stand (Site 2), of lower density from 20 July until 20 November 1978 during which time samples were taken on four occasions.

Rhizomes were forked up at intervals and after washing, 100 2 cm single-node lengths were selected from each of the four replicates. During all preparation work, the rhizomes and cut sections were kept in damp cheese cloth to prevent desiccation. Only sections with unsprouted and undamaged buds were used. The 100 sections of each of the four replicates were placed on dampened blotting paper in four shallow plastic trays, covered with glass and incubated in darkness at 25^{o}C for ten days. The percentage of buds that sprouted (exceeded 3 mm in length) was determined and the dry weights of the shoots recorded.

The data from the two sites were subjected to separate analyses of variance to determine the significance of changes in bud activity with time. The percentages were arcsine-transformed before analysis but the presented means and their 95% confidence limits are the back-transformed values.

The rhizomes sampled from both sites had grown during the previous autumn/winter periods and emerged and formed flower stems from October onwards.

5.4.2 Results

There was a significant downward trend in the percentage of buds forming shoots (bud activity) during December, January and February 1977 (Site 1) and again in November 1978 (Site 2) (Fig. 5.13). Coincident with the reductions in bud activity was a decline in the dry weight of the shoots. It was apparent that the reductions in bud activity and shoot vigour occurred while stem elongation was proceeding (Fig. 5.13).

5.5 EXPERIMENT 4. THE EARLY DEVELOPMENT AND GROWTH OF PLANTS REGENERATING FROM RHIZOME FRAGMENTS PLANTED AT TWO TIMES OF THE YEAR.

5.5.1 Materials and Methods

Two experiments of the same design were initiated to assess the

developmental pattern of plants regenerating from rhizome fragments. They were carried out in the field on a Wakanui silt loam soil in the summer of 1978/79 and the autumn and winter of 1979. Several weeks after rotary hoeing to 10 cm, the field sites were divided into parallel strips (blocks) 30 cm wide and 690 cm long. Each of these strips was then divided into 12, 30 x 30 cm areas (plots), separated from each other by 30 cm borders. The harvest times were allocated at random to the 12 plots within each block. The blocks were arranged into three groups of two, with 100 cm between these groups to provide walking space and 20 cm between blocks within each of the three groups to prevent disturbance of adjacent plots during harvesting.

On 14 November 1978 after hand hoeing to destroy emerging weeds, five 10 cm rhizome fragments were planted at a depth of 5 cm into each plot, using the tool described in Appendix XX. The rhizome material was obtained from a field population growing on the College farm. Ten-cm sections were taken from the central regions of rhizomes in the manner described for Experiment 2 of this Chapter. Only sections with healthy, unsprouted buds were used and during both the collection and planting procedures, the rhizomes were kept moist by wrapping them in damp cheese cloth. The mean dry weight planted fragment^{-1} was 0.213 g $\pm$ 0.068 (one standard deviation) and the mean number of buds fragment^{-1} was 3.9 $\pm$ 1.11, based on a sample of 30 pieces.

The experiment was harvested initially on 26 November 1978 and subsequently at six-day intervals until 1 January. Seven harvests were sufficient to provide the information required from this experiment. During the experimental period, weeding was accomplished by hand and irrigation was supplied by overhead sprinklers when necessary.

The second experiment was planted on 17 April 1979 in the same manner as described above. The rhizome material was collected from residual plants of the summer planting. The mean dry weight rhizome fragment^{-1} was 0.171 g $\pm$ 0.078 and the mean number of nodes fragment^{-1} was 4.1 $\pm$ 1.17, based on a sample of 30 fragments.

The first harvest was made on 30 April 1979 and thereafter samples were taken at somewhat irregular intervals owing to weather conditions, until 30 September when the final (11th) harvest was made. Irrigation was

unnecessary but the plots were hand weeded on several occasions during the experiment.

At each sampling occasion of both plantings, the following measurements were made: number of vertical shoots plot^{-1}; number of emerged shoots plot^{-1}; number of leaves shoot^{-1}; dry weights of planted rhizome, vertical underground stems, tops, new rhizome and roots plot^{-1}. Also at each sampling occasion, the occurrence of new rhizomes on all individual shoots was recorded.

5.5.2 Results

Soon after planting on 14 November 1978, shoots began to develop from some of the axillary buds. The total number of shoots representing about 60% of the planted buds, was determined very soon after growth began and there was subsequently no further shoot formation (Fig. 5.14); the other buds remained dormant throughout the period of observation. However a minority of the buds which remained dormant grew out horizontally and formed new rhizomes after considerable top growth had occurred (Fig. 5.18 e).

The growing vertical shoots elongated and emerged from the soil at different rates so that it was not until 26 December that 100% of the shoots had emerged (Fig. 5.14). This variation in rate of shoot emergence proved to be due to variation between fragments and between shoots within individual fragments.

The changes in the dry weight of different plant parts during regeneration are shown in Figure 5.15. It was evident that the planted rhizomes declined in dry weight during the early stages of development and indeed, the whole plants did not show a net increase in dry matter until 14 December. Total plant dry weight reached a minimum on 2 December and planted rhizomes were at their lowest dry weight on 14 December. Soon after the dry weight minimum of planted rhizome was passed, new rhizomes were initiated in the axils of the lowest leaves and from buds further down on the vertical shoots. At this stage the mean number of leaves emerged shoot^{-1} was 4.4 (Fig. 5.15). There was an interval of 30 to 36 days between planting and the formation of the first new rhizomes. Once the dry weight minimum had passed and new rhizomes were

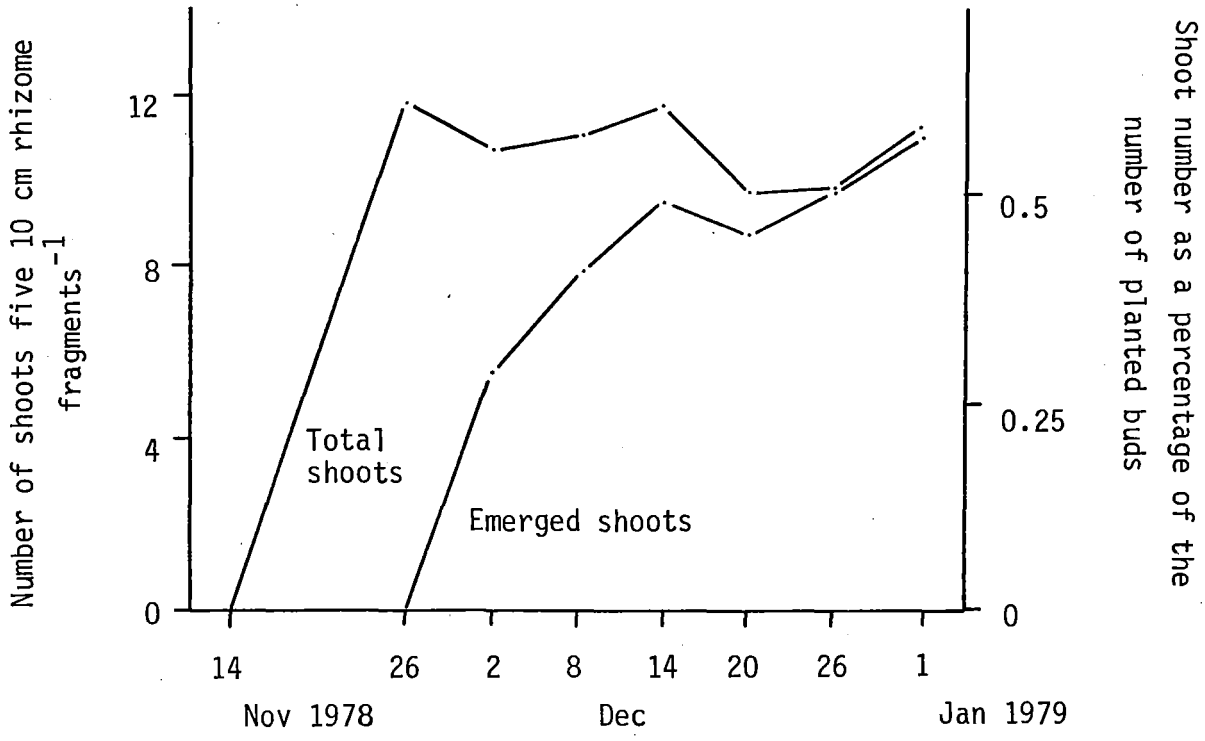


Figure 5.14 The development and emergence of shoots from 10 cm rhizome fragments planted 5 cm deep on 14 November 1978. Points are means of 6, 5 - plant replicates. (See Appendix XXX).

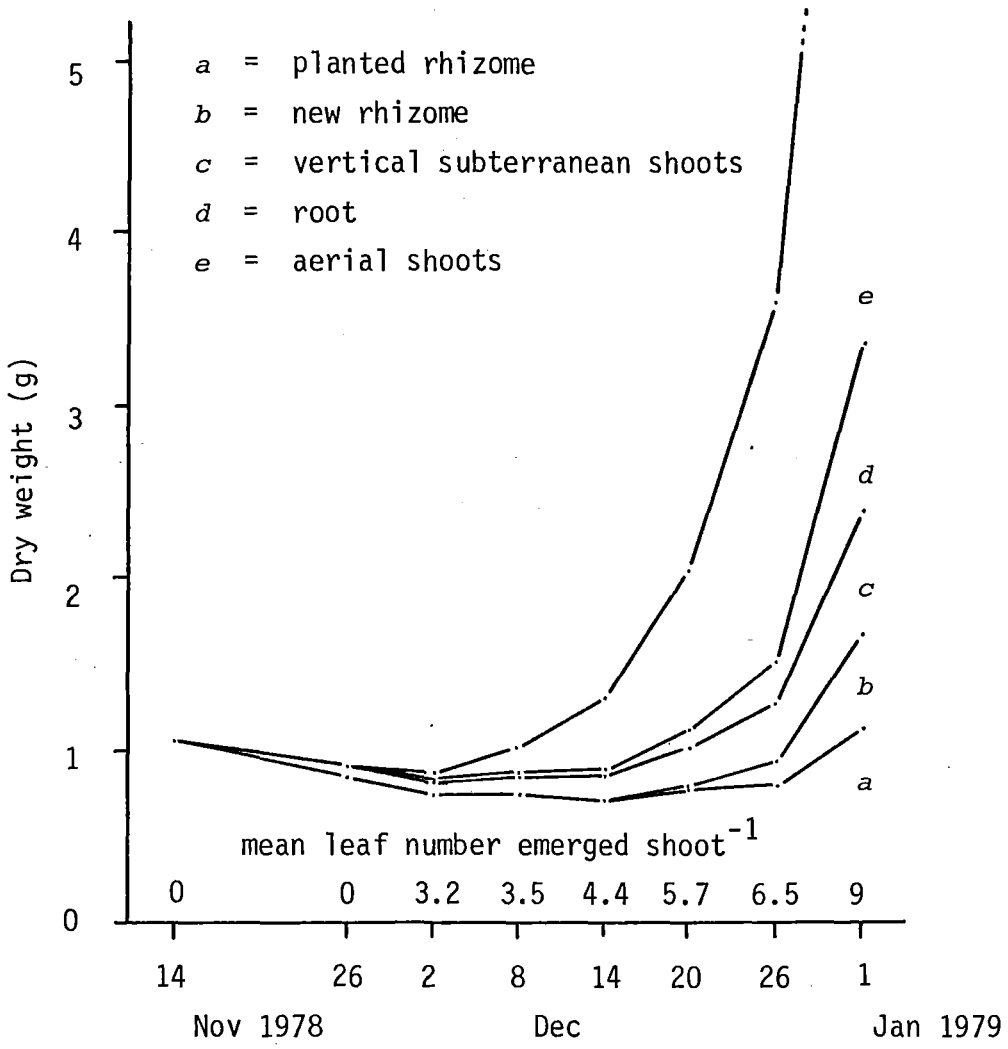


Figure 5.15 Changes in dry weight of different plant parts during the early course of undisturbed development and growth from 10 cm rhizome fragments planted on 14 November 1978. Points are cumulative dry weights of means of 6, 5 - plant replicates. (See Appendix XXX).

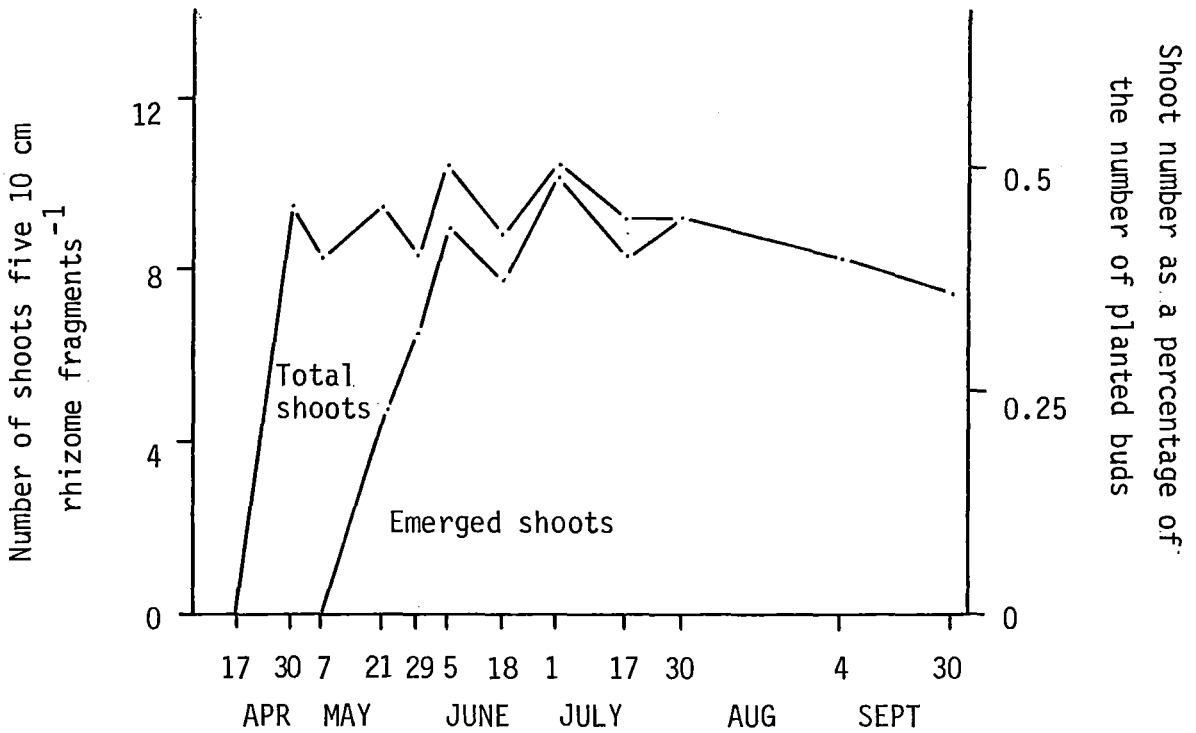


Figure 5.16 The development and emergence of shoots from 10 cm rhizome fragments planted 5 cm deep on 17 April 1979. Points as in Figure 5.14. (See Appendix XXX).

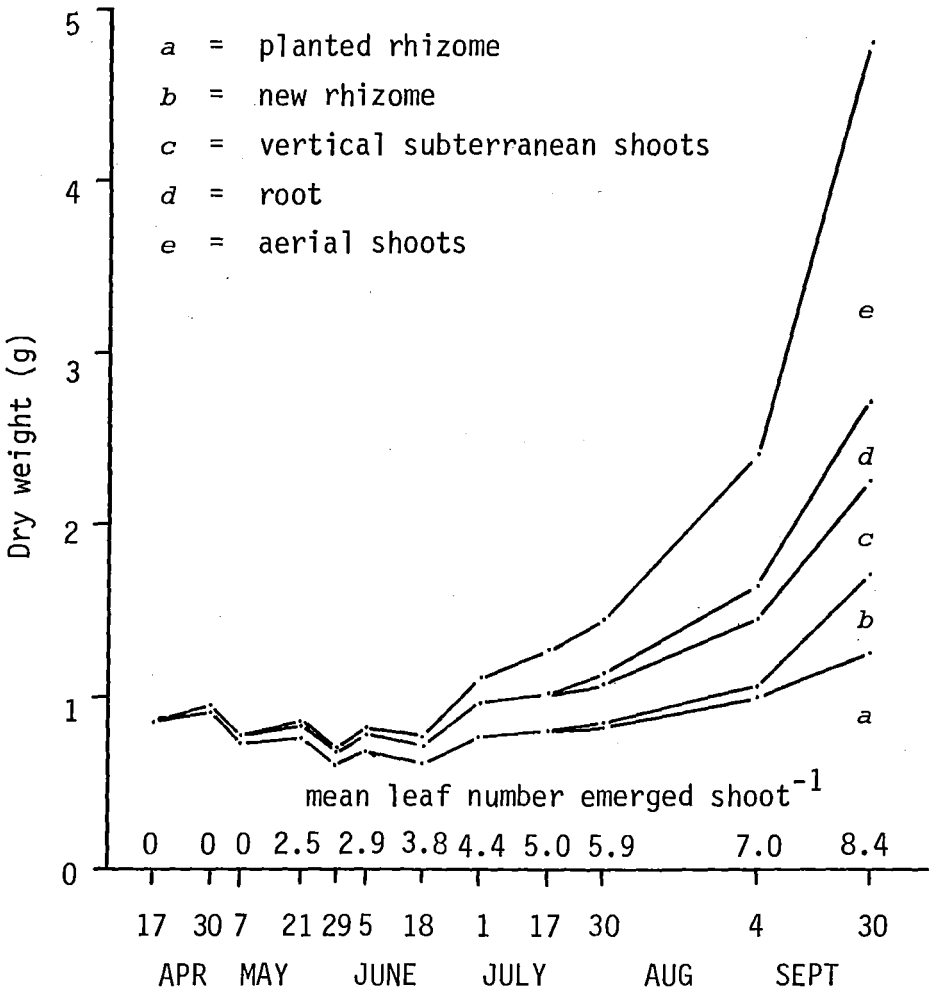


Figure 5.17 Changes in dry weight of different plant parts during the early course of undisturbed development and growth from 10 cm rhizome fragments planted on 17 April 1979. Points as in Figure 5.15. (See Appendix XXX).

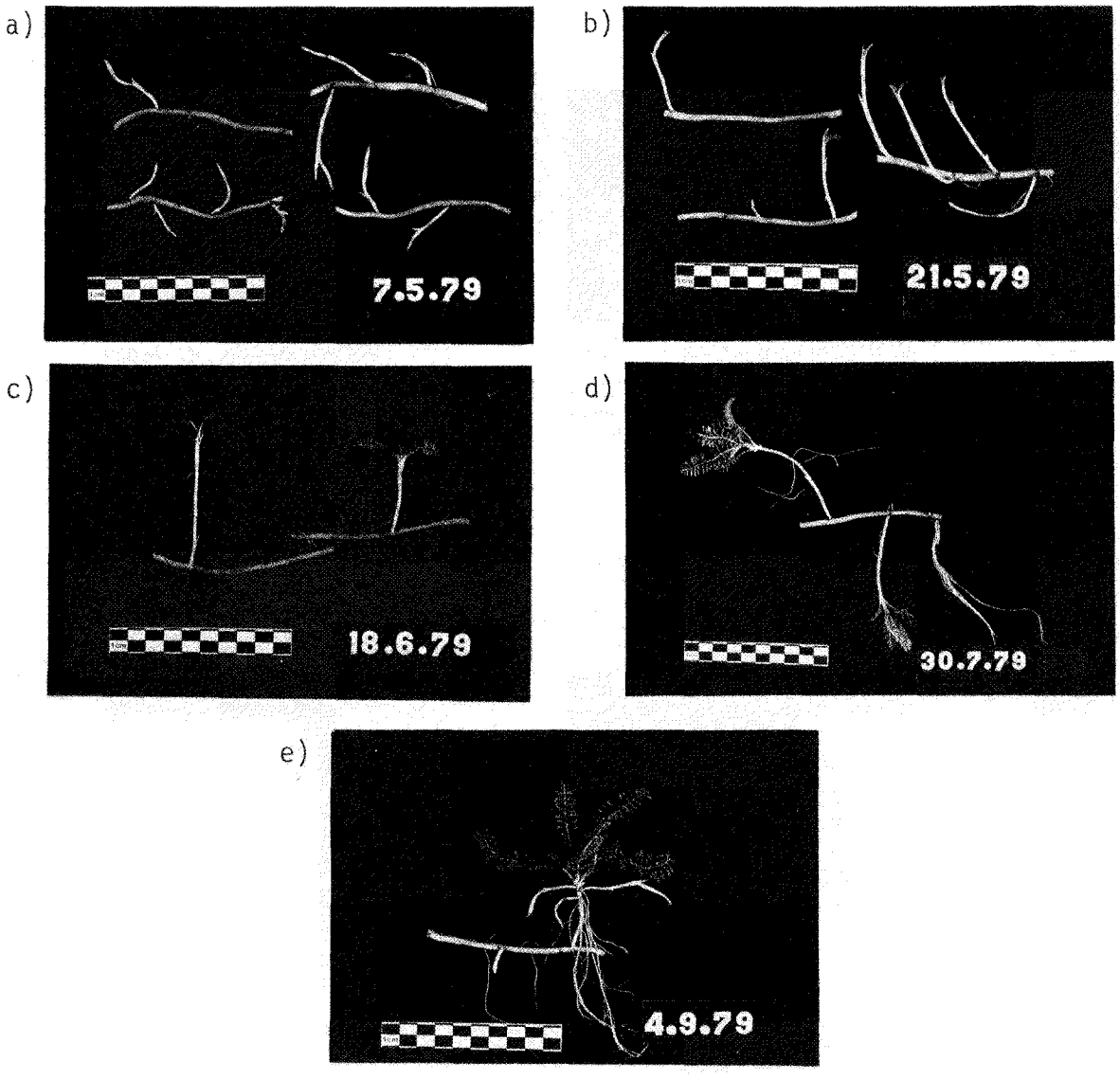


Figure 5.18 Stages in the development of plants from autumn-planted (17 April 1979) rhizome fragments. cf., Figures 5.16 and 5.17. a) shoot development prior to emergence; b) formation of first aerial leaves; c) minimum dry weight of planted rhizome fragments; a mean of 4 leaves shoot^{-1}; d) root formation from internodes of vertical shoots and basal end of planted rhizome fragment. Rhizome initials forming in axils of lowest leaves; e) new rhizome formation from buds on vertical shoots and from buds on planted rhizome fragment.

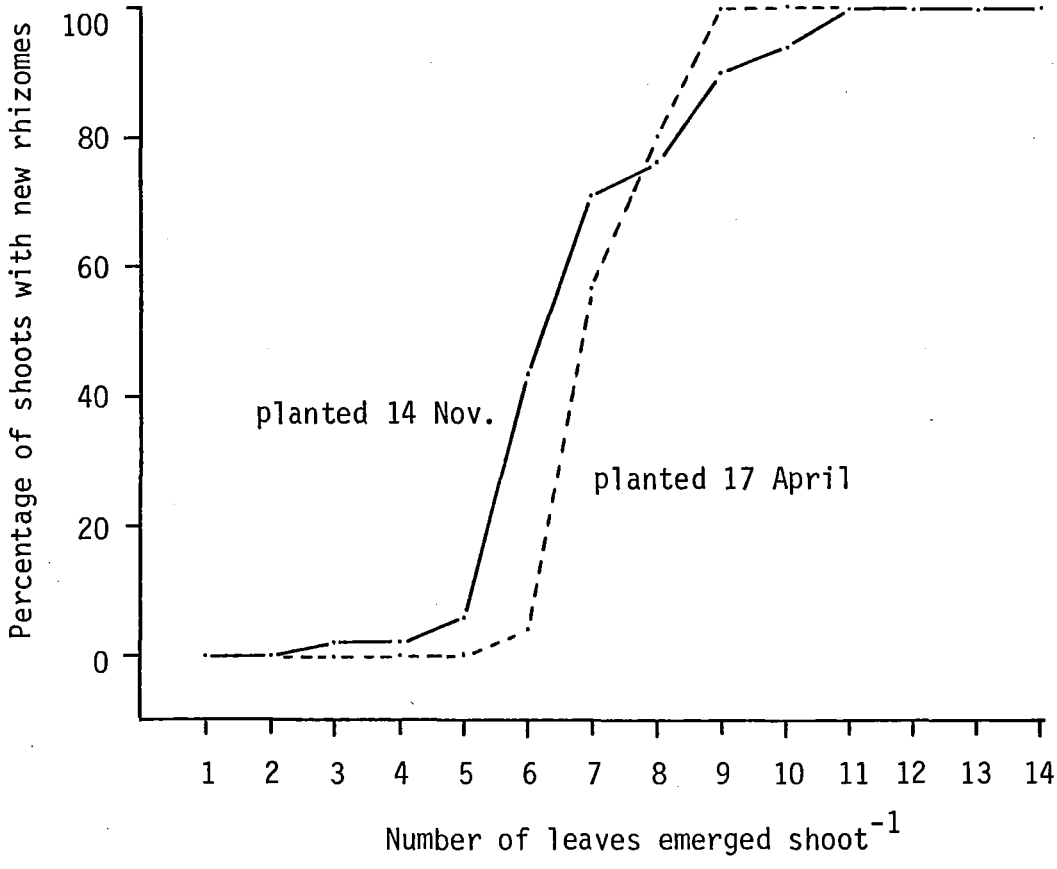


Figure 5.19 The percentage of shoots with new rhizomes in relation to leaf number emerged shoot^{-1} on 10 cm rhizome fragments planted on 14 November 1978 and 17 April 1979. (See Appendix XXXI).

developing, a phase of rapid dry weight increase began; the planted fragments also increased in weight (Fig. 5.15).

In Figures 5.16 and 5.17 are presented the results of the autumn planting. The developmental pattern of these plants was in all respects similar to the sequence in the summer-planted material except that the growth processes were considerably slower owing to the lower soil temperatures during this period. The developmental sequence thus occupied a greater amount of time. New rhizomes were again initiated soon after a dry weight minimum of the planted rhizomes was passed, when there was a mean of 4.4 leaves shoot^{-1} (Figs. 5.17; 5.18 c). An interval of 75 to 91 days had elapsed before rhizome initiation began in early July (Fig. 5.18 d). It can be seen from Figure 5.16 that approximately 40 to 50% of the planted axillary buds formed shoots and as in the summer planting, shoot emergence continued until 100% of the developing shoots had emerged.

Although new rhizomes were being formed in the plots when the mean number of leaves shoot^{-1} was 4.4, they were rarely present on individual shoots until the leaf number exceeded five on the shoots establishing during the summer, and six on winter-establishing shoots (Figs. 5.18 c; 5.19). As more leaves were produced, rhizome initiation occurred more frequently and all shoots with nine to eleven leaves had formed new rhizomes.

5.6 DEPTH DISTRIBUTION OF RHIZOMES

General observation has shown that the rhizomes of yarrow do not penetrate deeply in cultivated soils. A one year old stand which had been established from rhizome pieces planted at 5 cm on a Wakanui silt loam was sampled on 1 October 1978 to determine the depth distribution of rhizomes. This was achieved by slicing out five 2.5 cm layers of top soil down to 12.5 cm, washing away the soil and determining the oven dry weight of rhizomes together with roots, in each layer. Five randomly choosen samples of 0.1 m^2 were taken from within the population. The results are presented in Figure 5.20 from which it can be seen that most of the rhizome dry matter was restricted to the top 5 cm of soil. A small proportion occurred below 5 cm indicating that some rhizomes had grown at a downward angle to the soil surface. Roots were not separated

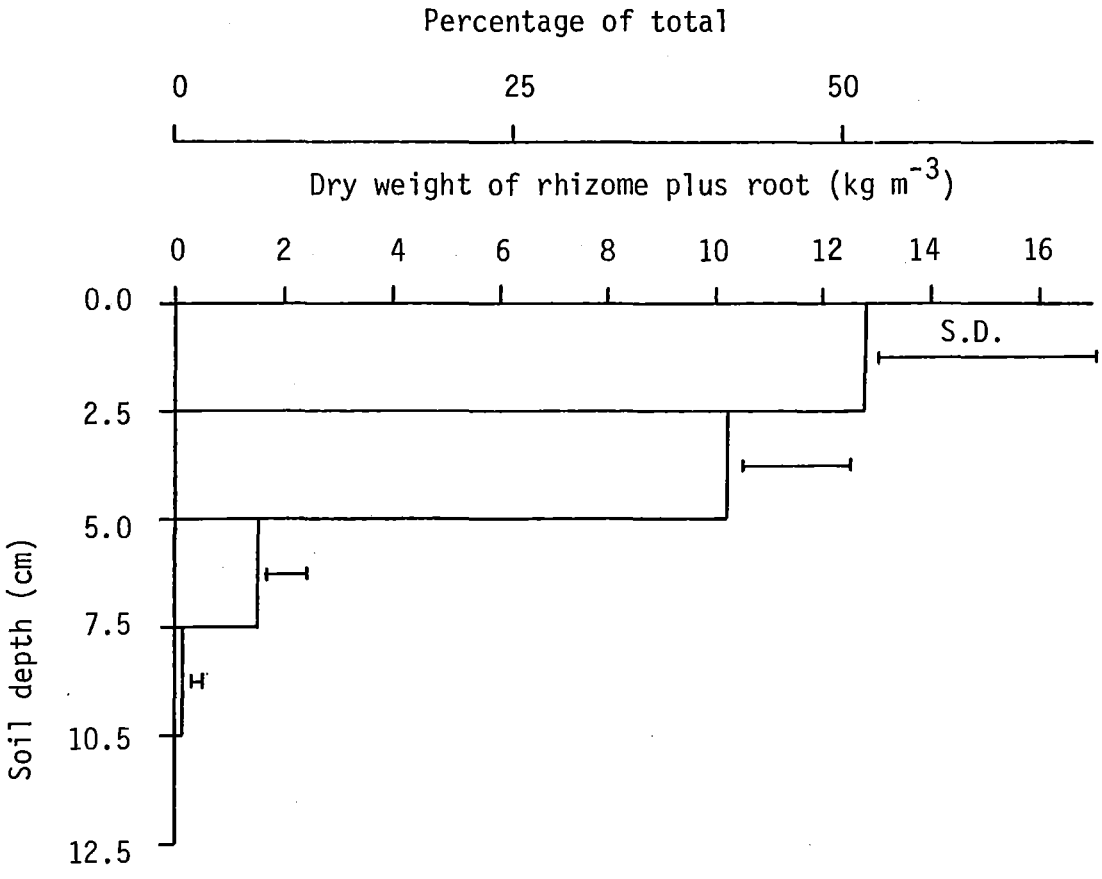


Figure 5.20 Depth distribution of rhizome and root dry matter after one season of growth in a Wakanui silt loam soil (See Appendix XXXII). There were five observations per sample and the horizontal bars are standard deviations of these samples.

from the rhizomes and constituted only a small proportion of the total weights.

5.7 DISCUSSION

Primary rhizomes were initiated on plants establishing from seed and from rhizome cuttings in Experiment 1, during the entire period of investigation (Fig. 5.1), indicating that plants from both types of propagule may add to the vegetative reproductive capacity of a field population, in their first season of growth. Elongation and lateral bud formation continued into the winter months (Figs. 5.2; 5.3) confirming the marked winter activity of rhizome growth demonstrated by field-grown plants in Chapter 4 (Fig. 4.34). In contrast, *Achillea millefolium* L. is winter-dormant in Britain (Fryer and Makepeace, 1977), possibly owing to the colder winter conditions experienced there.

Activity of the rhizomes was confined almost completely to the growth of apical buds, and hence elongation of the primary rhizomes, while lateral axillary buds displayed a remarkeable degree of inactivity (Figs. 5.4; 5.6); 97% of the buds remained inactive throughout the period of investigation in Experiment 1. The axillary buds on intact rhizomes of *Agropyron repens*, a pernicious grass-weed in many temperate countries, show a similar level and persistence of inactivity (Johnson and Buchholtz, 1962), attributable to apical dominance. It would seem that in yarrow, this phenomenon was also the result of an intense apical dominance, because when the influence of the apical bud was removed owing to insect damage to the bud itself, or to an internode some distance back from the apex, lateral bud growth occurred (Fig. 5.5). Secondary rhizomes were also produced from axillary buds when the rhizome apex was damaged upon contact with the wall of the growth container. Further evidence of the correlative nature of bud inactivity was given by the ability of the inactive buds to sprout and form vertical shoots when isolated on single-node rhizome sections (Fig. 5.13) and when isolated from the apical bud on multinode sections (Fig. 5.9). In a field situation, rhizome extension and therefore the lateral spread of plants would be assured despite insect attack and physical impediments to rhizome growth such as stones and localised soil compaction.

During the autumn and winter, when rhizome extension growth was vigorous, the apices remained below the soil surface (Fig. 5.6 a) and apical dominance was strong. However, when the rhizome apices emerged from the soil (Fig. 5.6 b), there was some relaxation of dominance and lateral buds grew out to form second order rhizomes with increasing frequency nearer the apical end (Fig. 5.7). Distinct polarity of bud growth, which also occurred when the yarrow rhizome apex was damaged (Fig. 5.5), has similarly been recorded in the rhizomes of *Agropyron repens* when the apex is removed from rhizomes attached to the parent plant (McIntyre, 1965; 1970), in isolated, decapitated rhizomes (McIntyre, 1971; Nigram and McIntyre, 1977) and in intact rhizomes in high humidity conditions (McIntyre, 1976). Chancellor (1974) also found that buds nearest the apical end of multinode rhizome fragments of *Agropyron repens* were more likely to become dominating than more basal buds which were usually inhibited. Leaky, Chancellor and Vince-Prue (1977 b) demonstrated that buds on single-node fragments from the apical region of rhizomes of *Agropyron repens* had the highest regenerative capacity. This polarity of bud growth, which seems to be typically associated with apical dominance in the rhizomes of *Agropyron repens*, has been ascribed to basipetally declining gradients of: nitrogen (McIntyre, 1971; Nigram and McIntyre, 1976), water content (McIntyre, 1976) and a gradient in the carbon : nitrogen (McIntyre, 1970). The mechanism of bud growth/inactivity in yarrow rhizomes was not the subject of investigation, but the similarity of the pattern of polarity with that in *Agropyron repens* does suggest that the mechanisms may be similar. An important consequence of this polarity, resulting in only a small proportion of axillary buds becoming active upon damage to, or emergence of the rhizome apex, is that conservation of buds and rhizome food reserves is assured, enabling an accumulation of regenerative potential, but at the same time, allowing continued extension of the rhizome system.

The *in vitro* activity of buds and the vigour of the shoots on single-node rhizome fragments of yarrow fluctuated seasonally and was greatest from March through until October, i.e. during the autumn and winter, and was least from November to February, the period when rapid aerial growth and new rhizome production were occurring (Fig. 5.13).

This pattern of growth potential, although not so marked, follows that described for the rhizomes of *Agropyron repens* by Johnson and Buchholtz (1962) in Wisconsin and by Leaky, Chancellor and Vince-Prue (1977 a) in Britain, and for the rhizomes of *Polygonum coccineum* (Lipke, Burnside and Haskins, 1965). The term, 'late spring dormancy' was used to describe this phenomenon in *Agropyron repens* to distinguish it from correlative inhibition and from the summer (Laude, 1953) and winter (Wareing, 1969) bud dormancies found in other species. This period of reduced bud activity, in *Agropyron repens*, characterised by a reduced percentage of isolated buds forming shoots, and by lower vigour of these shoots, has been shown to be coincident with a low level of nitrogen in the rhizomes (Lipke *et al.* 1965; Leaky *et al.* 1977 a) and also with the period of rapid growth of tops and new rhizomes (Johnson and Buchholtz, 1962). The decline in nitrogen content was considered to have resulted from rapid translocation of almost all available nitrogen from old rhizomes, for the spring flush of growth (Leaky *et al.* 1977 a). Other authors, working with different species have similarly shown periods of low regenerative capacity to be coincident with the flowering periods, with maximum regenerative potentials occurring during the winter when nutrient demand is presumably lower (Graham, 1936; Hudson, 1953; Dore, 1953; Raju, Steeves and Coupland, 1964; Henson, 1971).

It would seem that such a period of low regenerative capacity might be exploited in a weed contol programme. For example, if cultivations were carried out during this period, then plants would not be able to re-establish and large numbers of buds and rhizome pieces would perish due to decay. It would also appear to be possible to take advantage of the lower vigour of shoots produced during the dormancy period for a crop sown at this time would be expected to be relatively more competitive against the weaker regrowth shoots. However, Leaky, Chancellor and Vince-Prue (1977 b) were able to completely overcome late spring dormancy in the rhizome buds of *Agropyron repens* by increasing the concentration of potassium nitrate to single-node fragments *in vitro*. Furthermore, Dexter (1936) found rhizome fragments of *Agropyron repens* regenerated more freely from fertilised populations and Leaky *et al.* (1977 a) were able to lower the incidence of late spring dormancy by applying nitrogen

fertiliser to their couch swards. It was therefore considered unlikely that this dormancy could be exploited successfully for weed control in agricultural systems where nitrogen fertilisers are used (Leaky *et al.* 1977 b). If the reduction in bud activity and shoot vigour in yarrow was also the result of a nitrogen shortage in the rhizomes as a consequence of the demand created by leaf and flower stem production, then it might also be expected to be dependent upon the soil nitrogen status and to have little utility for the control of yarrow in fertile soils. Moreover, the small reduction in bud activity and shoot vigour in yarrow rhizomes (Fig. 5.13) in comparison with the much more pronounced effects with *Agropyron repens*, adds weight to this contention.

Because there is no period of pronounced innate dormancy in the rhizome buds of yarrow, disturbances at any time of the year which interfere with the dominating influence of the apical bud, will allow immediate bud activity and re-establishment of the population. This must allow yarrow to establish with crops planted at any time of year, and also indicates that successful cultural control, approaches to which are discussed later in this section, may be possible throughout the year.

The cultivations associated with management of arable land will fragment the rhizomes of yarrow to various extents, and the pieces will be distributed throughout the cultivation profile. In order to gain an understanding of the way cultivations may influence the survival of a population, rhizome fragments of different lengths were planted in soil at depths down to 30 cm (Experiment 2).

All rhizome fragments died without producing shoots when placed on the surface, (Fig. 5.8 a) and this was attributed to desiccation, although 5 days of heavy rain, which caused the ground to become water-logged, began 12 days after planting (Appendix XXVI). This might suggest that control of the rhizomes could be achieved by exposing them at the surface, and that long periods of dry weather may not be necessary for fatal desiccation. However, Hilgendorf and Calder (1952) have noted that it is extremely difficult to bring all rhizomes to the surface on account of their brittleness, which results in many small but viable pieces remaining below the soil surface in conditions conducive to regeneration.

At a depth of 2.5 cm, a high percentage of rhizome fragments survived to form aerial shoots, but survival declined with increased depth of planting and more rapidly the shorter the fragment, until at 20 and 30 cm no fragments survived (Fig. 5.8 a). The failure of individual fragments to produce aerial shoots cannot be attributed to a lack of bud viability in view of the high survival at 2.5 cm, but was considered to have been caused by three major factors : reserve exhaustion, pathogenic soil organisms, and gradients in environmental conditions down the soil profile. Before discussing these factors and how they may have been responsible for the observed pattern of rhizome survival, the possible consequences of the waterlogging need to be contemplated. Rainfall amounting to 112 mm occurred between 10 and 14 December, inundating the entire experimental area for several days during which the shoots from the 2.5 cm depth were beginning to emerge. On 21 December a further 28 mm fell. The water drained within a few days, out of the top few centimetres of the soil and continued to move slowly out of the burial profile over a period of three to four weeks. It is argued that anaerobic conditions prevailed for an increasing period of time with increasing depth in the soil so that the 'normal' pattern of rhizome survival was modified to an increasing degree with increase in planting depth. This modification, the extent of which remains unknown, is presumed to have taken the form of death of buds, shoots and rhizome fragments owing to a lack of oxygen. Rhizomes retrieved from 20 and 30 cm were either completely decayed, identifiable only by the remaining strands of fibrous material, or were judged to be dead, though undecayed, with short vertical shoots, the growth of which had clearly been curtailed shortly after it had begun. It was considered that free water remained at these depths for long enough to have caused the death of all fragments and shoots.

Substantial compaction and caking of the soil also resulted from the soil having been waterlogged, an effect which would have increased the physical resistance experienced by the growing shoots. The reduction in emergence of shoots at 10.0 cm depth (Fig. 5.10) was ascribed to soil compaction because unemerged shoots were crumpled as would have been expected as the result of the physical impediment of compacted soil. Shoots from 2.5 and 5.0 cm probably had emerged before the soil became hard enough to limit their passage.

Within the depth range, 2.5 to 10.0 cm, death of shoots and rhizomes due to waterlogging was thought to be minimal and the survival response of the fragments (Fig. 5.8 a) was attributed mainly to other factors. A primary cause of the failure of rhizomes to survive at 5.0 and 10.0 cm was possibly the effect of pathogenic soil organisms attacking either the growing shoot or rhizome fragment before the shoot was able to emerge from the soil. Shorter fragments had a lower survival than longer fragments (Fig. 5.8 a) and it is suggested that part of the reason for this phenomenon is that the shorter the fragment the more easily would it be rendered unable to form an aerial shoot as a consequence of the low number of potential shoots (buds).

The exhaustion of rhizome food reserves by shoots before emergence may have also played an important role in the survival of fragments. Owing to the decreasing percentage of buds forming shoots the longer the fragment (Fig. 5.9), it is presumed that shoots growing from long fragments had a greater supply of rhizome reserves than shoots on short fragments. Consequently, the former were able to grow further through the soil before exhausting reserves. This may partly explain why fewer 4 cm fragments survived, i.e. formed aerial shoots, from 5.0 cm than 16 cm fragments. It is clear that this effect would be more pronounced with increasing planting depth as is indicated in Fig, 5.8 a.

Inspection of the pattern of bud activity evident on the fragments which had remained undecayed by the time of the sampling, showed a greater percentage of planted buds became active the shorter the fragment length and the more shallow they were buried (Fig. 5.9). The decline in bud activity with depth of burial could have been caused by a number of factors which would have been expected to exhibit a gradient within the soil profile, e.g. oxygen and carbon dioxide tensions, and temperature. Johnson and Buchholtz (1961) demonstrated that rhizome buds of *Agropyron repens* have a definite oxygen requirement for activation, and it seems reasonable to suggest that the buds of yarrow may behave similarly.

The decline in bud activity with depth of burial observed on the undecayed pieces, may have been an important factor in the decline in rhizome survival with increasing depth (Fig. 5.8 a) especially of the shorter fragments. That is, as there was only an average of 1.3

buds 4 cm fragment^{-1}, the decline in activity to 55% at 10.0 cm depth (Fig. 5.9) resulted in some 4 cm fragments without shoots and thus unable to survive.

The decrease in the percentage of buds becoming active with increasing length of fragment (Fig. 5.9) was attributed to re-establishment of a correlative mechanism amongst the buds and developing shoots. This phenomenon has also been demonstrated in *Agropyron repens* (Chancellor, 1968; 1974; McIntyre, 1972; Leaky, Chancellor and Vince-Prue, 1978 a) and in *Sorghum halepense* (Hull, 1970). It not only limits growth to a proportion of the buds on multinode rhizome sections and therefore, as already discussed, probably allows emergence of shoots from greater depths, but also conserves buds and reserves, and hence regenerative potential in the face of cultivations. Residual buds were not tested for viability, but they were considered to be in a healthy and viable state at time of sampling, 103 days after planting.

Although the survival of rhizome fragments declined with decrease in length and increase in depth below 2.5 cm (Fig. 5.8 a), the numbers of shoots arising from a fragmented rhizome system will be more important in determining the effects of a cultivation on a population. For example it was shown that only 5% of 4 cm pieces survived at 10.0 cm, whereas 55% of 16 cm pieces survived (Fig. 5.8 a). But if a field population was fragmented severely, there would be many more fragments than if the same population was fragmented to a lesser extent. The greater death rate of smaller fragments may conceivably be compensated for by the larger numbers of pieces, resulting in as many shoots emerging from a given depth after severe and mild fragmentation. Such compensation did occur in Experiment 2 for at a depth of 10.0 cm a similar proportion of the planted buds produced aerial shoots from both 4 and 16 cm pieces (Fig. 5.8 b) despite the reduction in fragment survival with decreasing fragment length (Fig. 5.8 a). At 5.0 and 2.5 cm depth, a considerably greater proportion of the planted buds produced aerial shoots from 4 cm than from 16 cm pieces (Fig. 5.8 b) although the percentage of fragments surviving declined with decreasing fragment length (Fig. 5.8 a). Thus a high degree of fragmentation may result in as many or more aerial shoots than less severe fragmentation, but there will be fewer residual buds available

for regeneration after further disruption.

It is often reported from agricultural practice, that the breaking of rhizome systems of rhizomatous plants such as *Agropyron repens* and yarrow, causes an increase in the growth of the plants. It has been argued that cultivations can assist in the increase of the weed population. The results of Experiment 2 have indeed shown that an increasing number of aerial shoots of yarrow will occur at shallow placement depths (2.5 to 5.0 cm) with increased severity of fragmentation, as a consequence of a reduction in apical dominance and reduction in its re-imposition. However, in a cultivation programme with the objective of exhausting the reserves of the yarrow rhizome system, the higher the proportion of buds that can be stimulated into growth the more the reserves and buds will be consumed. Therefore, severe fragmentation, as achieved by rotary cultivation (Fail, 1956), plus shallow burial would be the most desirable initial manipulation. The timing of following cultivations which are required to destroy the young regenerating shoots and hence allow further exhaustion of remaining viable rhizomes and buds by stimulation of hitherto inactive buds, will be critical if the least number of implement passes are desired. If the second disturbance is not carried out until after new rhizomes are formed, then this new store of buds and reserves will necessitate more work for complete exhaustion. On the other hand, if very frequent cultivations, say every one or two days, are carried out, the desired result will be achieved, but many of the passes will have been unnecessary.

The work of Hakansson (1967) with *Agroypron repens* showed that buried rhizome fragments initially declined in dry weight as regeneration proceeded and reached a minimum just prior to the formation of new rhizomes. Carbohydrate and nitrogen reserves of the planted pieces were also at a minimum at this stage. He found that the success of reburied pieces was lowest at this stage owing to the depleted reserves available to regenerating shoots. Regenerating yarrow plants (Experiment 4) followed a similar pattern of early development with the planted rhizome pieces reaching a minimum dry weight just before the formation of new rhizomes. This stage was recognised in summer and autumn-planted populations when there was a mean of four to five leaves rosette^{-1}. It is therefore argued

that if a procedure of exhaustion were to be followed, the most appropriate stage to re-disturb the plants after the initial cultivation, would be just prior to the formation of new rhizomes, when the buried fragments are at their lowest dry weight, and presumably their lowest regenerative potential. Time required to reach this stage of development will vary according to the prevailing growth conditions, being shortest in the summer (30 to 36 days) and longest in the winter (75 to 91 days). To achieve complete exhaustion in the shortest possible time, optimum growth conditions would be necessary.

The success of cultivations aimed at exhausting rhizome reserves will depend upon the thoroughness of fragmentation and hence the ability of cultivating implements to reach the deepest rhizomes. The observations of part 5.6 showed that, in a lose soil, few new rhizomes occurred below 5 cm when the original planted pieces had been placed at 5 cm (Fig. 5.20). Therefore few rhizomes had grown at an angle less than horizontal. Although rhizomes may be initiated at greater depths on vertical shoots arising from more deeply buried rhizome fragments, the foregoing results suggest that in undisturbed stands, rhizomes probably remain in the top few centimetres of soil. It would seem therefore that yarro rhizomes are likely to occur predominantly within easy reach of cultivating implements.

Where no effective exhaustion of the rhizome system can be achieved by repeated cultivation, the combined effects of burial, fragmentation and crop competition could be exploited. Increasing depth of burial not only resulted in a marked reduction in the percentage of buds forming aerial shoots (Fig. 5.8 b) but also rendered the emerged shoots much less vigorous as determined by the total dry weight and new rhizome dry weight per aerial shoot (Figs. 5.11; 5.12). Shoot vigour also tended to be reduced with reduced fragment length at a depth of 10.0 cm, and 4 cm pieces at this depth were unable to flower (Table 5.2). Reduction in vigour with increased depth was due to delayed emergence, whilst the reduction with decreasing fragment length at 10.0 cm depth may have been the result of lower reserves per shoot. A crop sown into soil immediately after yarrow rhizomes had been disturbed would be likely to gain a greater competitive advantage over the yarrow, the more deeply the rhizomes had been buried and the more they were fragmented.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

An awareness of the phenological development of a weed is an essential step towards understanding how it is able to survive the disturbances of the agricultural environment, and hence is also a prerequisite in the formulation of measures whereby populations of its species may be either restricted in size, or eliminated from an area. The observations and measurements made throughout this study that relate to the timing of major events in the life history of yarrow, made possible the construction of a simple life history diagram (Fig. 6.1). This represents the development of yarrow in the rather hypothetical situation of an undisturbed, competition-free environment. In the arable farm environment, stages in this development may be promoted, restricted or prevented, or shifted in time as a result of the many manipulations and disturbances associated with this system. Figure 6.1 will be referred to in this Discussion as points concerning the phenology of the plant arise.

6.1 RHIZOMES

Several authors have referred to the ability of yarrow to regenerate from rhizome pieces. It is inferred from the comments of Hilgendorf and Calder (1952), that rhizome pieces remaining below the soil surface after cultivation, readily form new plants. Reynolds (1961) observed that the plant was spread by cultivations which break up the rhizomes and scatter the pieces, each it was said, being capable of establishing a new plant. The results of experiments in this thesis have confirmed that axillary buds on the rhizomes form vertical shoots once they have been isolated on single or multinode rhizome fragments (Fig. 5.8 b; 5.13; 5.14; 5.16). Such regeneration is possible because a large proportion (> 90%) of the buds on intact rhizomes attached to the parent plant, remain dormant, apparently as a consequence of apical dominance (Fig. 5.6), until this effect is negated by fragmentation of the rhizome or damage to the apical bud.

Comment has been made in the literature on the potential of yarrow to survive after several consecutive cultivations. Connell (1930) consider-

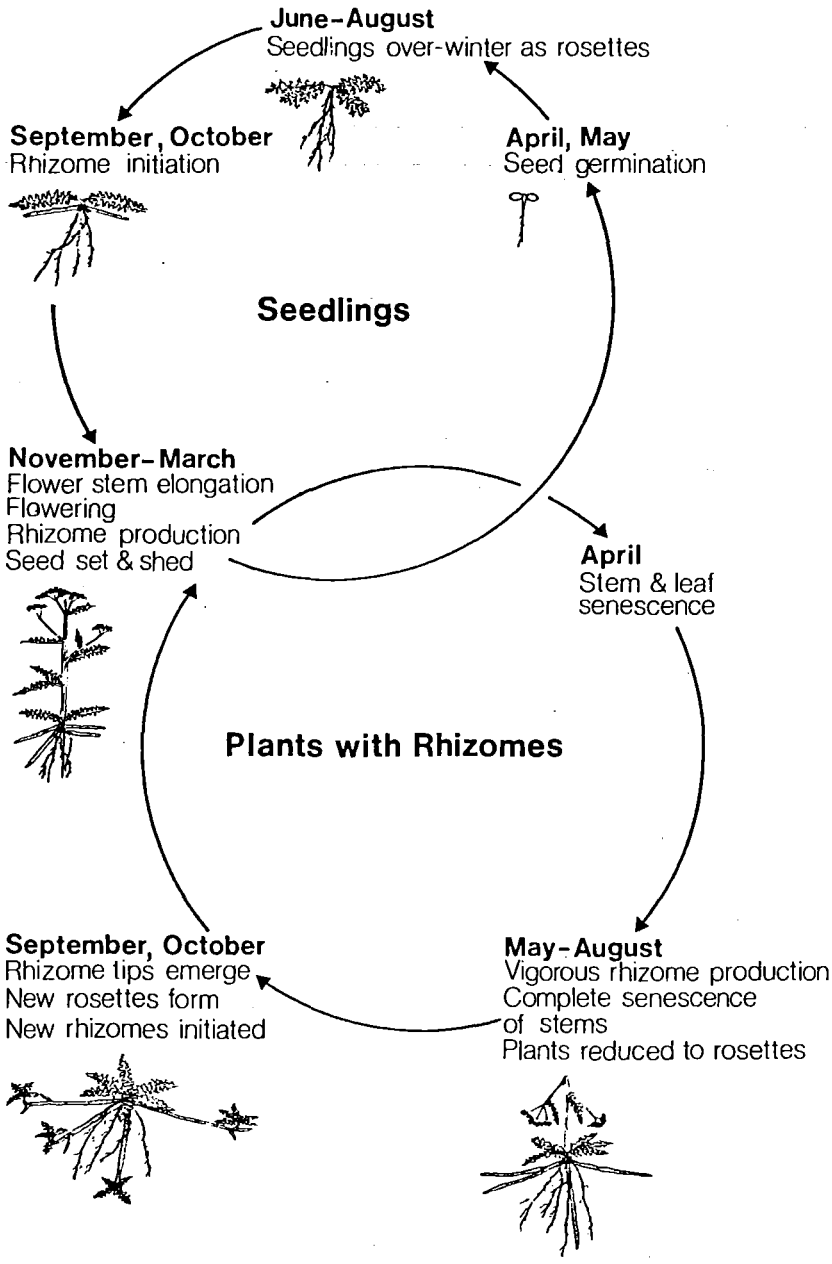


Figure 6.1 Life history of yarrow

ed that summer cultivations only weakened the plant, which was still able to regenerate in the following autumn. Similarly, Bourdôt and Butler (unpublished) found rhizomes were still capable of regenerating after three rotary cultivations. The mechanism for this ability to preserve potential regrowth is apparently the retention of a percentage of buds in a dormant condition on rhizome fragments (Figs. 5.8 b; 5.9; 5.14; 5.16). This phenomenon also occurs on fragmented rhizomes of couch (*Agropyron repens*) (Chancellor, 1968) and is caused by the re-imposition of a dominance system amongst the developing shoots (Chancellor, 1974). A similar mechanism is probably involved in the fragments of yarrow rhizomes but it would seem to differ in that buds either grow, or they do not, and those that do, continue on to form aerial shoots (Figs. 5.14; 5.16), rather than one becoming dominant and the others stopping growth in a sequence as shown for couch (Chancellor, 1974). However, the result of fragmentation of the rhizomes of both species is the conservation of a percentage of the buds which remain capable of regenerating upon destruction of the first-formed shoots, or after further breakage of the rhizome fragment.

In regions of seasonal growth, the ability to grow or reproduce in the winter season, may greatly aid the spread of a weed. In Britain it has been observed that many weed species are able to establish, grow and even reproduce, in autumn and winter after the harvest of many crops (Bunting, 1960). This phenomenon also occurs in the New Zealand weed flora. Seasonal activity of growth in the *Achillea* genus varies from race to race. Clausen, Keck and Hiesey (1958) found two hexaploid Danish races to be continuously active throughout the year when transplanted in California, but *Achillea millefolium* L. becomes dormant during the winter in Britain (Fryer and Makepeace, 1977). The New Zealand Department of Agriculture (1924) however, commented that the autumn growth of yarrow in New Zealand was greater than that of lucerne (*Medicago sativa*) and was thus likely to succeed at the expense of the lucerne if not adequately controlled prior to sowing. Results presented in this thesis substantiate that yarrow is active during the autumn and indeed, most remarkably, during the entire winter period in Canterbury. The most significant feature of this cool season activity is the extreme vigour of rhizome growth (Figs. 4.32; 4.35; 6.1), which can allow rapid increase in the regenerative potential, and occupation of the habitat during a period when many competitors are relative-

ly dormant, e.g. grasses and clovers, or absent, such as in the undisturbed stubble of a summer crop. The implication is that control measures should be taken in the late summer or early autumn, as soon after the crop harvest as possible, rather than leaving an infested stubble undisturbed. Less effort would presumably be required in reducing the rhizome bud numbers in the soil at this time than in the following spring, by which time the dry weight of rhizomes may have increased sixfold (Fig. 4.32). Furthermore, a consequence of incorporating large amounts of rhizome (and other plant material) into the seed bed immediately prior to sowing the crop seed in the spring, may be a substantial reduction in the yield of the crop. This point is expanded later in this Discussion.

Some authors have indicated that cultivations may have a detrimental effect on the survival of yarrow. Connell (1930) and Hilgendorf and Calder (1952) considered that multiple summer cultivations give some contol of the plant. Bourdôt and Butler (unpublished) found that two passes with a rotary hoe spaced eight weeks apart in the spring resulted in significantly less regrowth in the stubble of a following barley crop, than a single pass, presumably owing to a greater exhaustion of buds and reserves. As cultivations may break rhizomes into various lengths and bury them at various depths, it is necessary to examine both the effects of fragment length and burial depth on the growth of rhizome buds in order to understand the mechanism of the response of the plant to soil disturbances. The results of Experiment 2, Chapter 5, showed that an increasing percentage of rhizome buds formed shoots as the fragment length declined while a decrease in the depth of burial also resulted in a higher percentage of buds forming shoots (Fig. 5.9). This relationship between bud growth and both fragment length and burial depth suggests that in a programme of cultivations aimed at exhaustion of the rhizome reserves, by alternately stimulating bud growth and destroying the shoots produced, initial cultivation should cause as severe fragmentation as possible and keep the fragments within close proximity to the soil surface.

There was 100% mortality of rhizome fragments planted on the surface due to desiccation (Fig. 5.8 a) but in practice, attempts to desiccate the rhizomes are thwarted by their brittleness, which prevents

all regenerative tissue from being brought to the surface (Hilgendorf and Calder, 1952). Therefore it is possible that attempts to exhaust, rather than desiccate the rhizome system, are more likely to be successful.

Experiment 2, Chapter 5, was designed with the additional aim of determining the maximum depth from which shoots could emerge from the various size rhizome fragments. Unfortunately, this objective was not realised owing to the death of fragments below 10 cm, most probably as a result of flooding (Fig. 5.8 a). The possibility of burying rhizome fragments below the depth from which they can emerge, justifies further work to determine the limits of shoot growth from rhizome reserves.

In view of the importance of regeneration from rhizome buds for the survival of yarrow in the face of cultivations, and the potential consequences of fragmentation of rhizomes during a period of innate bud dormancy, should this occur, single-node fragments were tested for their ability to produce shoots at intervals over a complete year. However, no pronounced period of innate dormancy was detected (Fig. 5.13), suggesting yarrow may regenerate readily throughout the year. This finding is not without significance for it indicates that cultivations to exhaust rhizome reserves may be effectively carried out at any time of year. It also helps explain the ability of yarrow to survive in the arable environment in which soil disturbances may occur at any time of year.

Saxby (1944) remarked that yarrow increases in frequently cultivated soils. It has been shown in this thesis that fragmentation of the rhizomes causes a proportion of the hitherto dormant buds to sprout and form shoots which grow to the surface (Figs. 5.13; 5.14; 5.16). It is inferred that the total bud reserve must decline if the young regenerating shoots are destroyed by further cultivations, stimulating more buds into growth. This would be the case if cultivations were repeated before new rhizomes were produced, but if the frequency of cultivation was such as to allow new rhizomes to form, then a rapid build up in the numbers of plants appearing after each cultivation would be expected. This may partly be the cause of increases in populations on cultivated soils. Therefore, in Experiment 4, Chapter 5, an attempt was made to define the stage at which new rhizomes are initiated by plants regenerating from rhizome fragments. It was shown that regardless of the time of year at which planting took

place, new rhizomes were initiated on the vertical shoots when these had developed five to six rosette leaves (Fig. 5.19). This result suggests not only that regenerating plants develop in a well defined pattern regardless of the time of year regeneration begins, but also that cultivations repeated after five to six leaves have formed would be likely to result in increasing numbers of plants.

Furthermore, at the stage when new rhizomes were initiated, the dry weight of the planted fragments had just passed a minimum value (Figs. 5.15; 5.17). It might reasonably be expected that the residual buds, if stimulated to grow at this time, would have the lowest possible level of stored reserves from which to draw upon. Such shoots would probably be less vigorous, less able to emerge, and be less competitive with a sown crop than either shoots stimulated at an early stage in regeneration, or those developing at a later stage from new rhizomes. Hakansson (1967) showed that *Agropyron repens* plants also reached a minimum dry weight near the time of initiation of new rhizomes and were most susceptible to reburial at that stage. It is therefore suggested, that if only a minimum of cultivation was to be carried out prior to sowing a crop, a final cultivation when the rhizome pieces were at their lowest dry weight would probably allow the crop to have a greater competitive advantage than it might otherwise have had.

The results of Experiment 2, Chapter 5, which demonstrated a considerable reduction in plant vigour with increased depth of burial from 2.5 to 10 cm (Figs. 5.11; 5.12) suggest the competitive ability of regenerating plants may also be considerably reduced by increasing the depth at which fragments are buried. The ease, however, with which fragments may be buried below 10 cm, for example, will depend upon the distribution of rhizomes in the soil profile. The greater depth of the profile they occupy, the more difficult it will be to plough their fragments below 10 cm. However, results presented in this thesis indicate rhizomes occur mainly within the top 10 cm of loose soil (Fig. 5.20) and therefore, providing they have not previously been buried by ploughing, efficient burial of fragments should be possible. Anderson (1927) noted that rhizomes were more shallow in compact soils which suggests they may be more shallow in pasture than in cropped soil, and as a consequence burial of all

pieces may be more readily achieved after pasture.

If exhaustion of rhizome buds and reserves is to be seriously considered as a means of controlling yarrow rhizomes, further research will be required. Of high priority should be the determination of the best implements to achieve maximum breakage of rhizomes and subsequent shoot destruction in various soil types. For example, discs may be more suitable on stoney soils than the rotary hoe for initial fragmentation, while a tined implement may be adequate for subsequent destruction of shoots on many soils. To effect control most economically, the period for which the land is fallow and the number of implement passes would be of great importance. For example, it may be possible to repeat cultivations before shoots reach the five to six leaf stage, hence reducing the time period of the fallow.

6.2 SEEDS

A very high output of seed in favourable environmental circumstances is often a characteristic of weedy species. Hanf (1974) estimated 3,000 to 4,000 seeds per plant could be produced by yarrow while Reynolds (1961) commented on the plant's free-seeding ability and establishment from seed in New Zealand. Approximately 23 ovules per capitulum were produced by plants in the English study of Bostock and Benton (1979) and similarly Bourdôt, White and Field (1979) found 25 florets per capitulum. The latter authors estimated that 2,800 seeds per stem could be formed, giving a potential of 900,000 seeds per m^2. Fryer and Makepeace (1977) considered reproduction by seed was very important in yarrow, but direct evidence of the importance of this method of reproduction was not obtained in the study presented in this thesis. However it was inferred from the very high seed output and high level of viability (Bourdôt, White and Field, 1979), that seed reproduction could be of considerable importance for the establishment of plants on arable land.

Discontinuous germination as a result of variable seed dormancy, and great longevity are often important attributes of weeds, allowing them to survive periods unfavourable to their growth. It has been reported that

freshly harvested yarrow seed has a high germination percentage (Yaskonis and Bandzaitene, 1979; Robocker, 1977; Bostock, 1978) and that viability may remain for a considerable period in the soil (Bostock, 1978). Bourdôt (unpublished) substantiated this latter contention when he found viable seeds in a fallow soil 21 months after plants last shed seed onto the area. Kannangara (pers. comm.) has shown the initial viability of nearly 100% remained when the seeds had been buried at 10 cm depth or greater for one year, supporting the previous claims of considerable longevity. It is probable therefore, that seeds may play an important role in the survival of the species, especially in situations where rhizome buds and reserves have been depleted by successful control measures.

A knowledge of the periodicity of weed seed germination has a most important practical application. Timing of cultivations to get the maximum weed destruction depends on knowing when the seeds germinate, and conversely, understanding the times when they will not germinate may save labour and expense. The seeds of yarrow were shown to germinate on bare ground, partly after fruiting and partly in the following spring by Dorph-Peterson (1925). This observation was considered explicable by Bostock (1978) in terms of the breaking of conditional dormancy of different types of seed with different requirements for germination. Similarly, field observations made throughout this study have shown freshly shed seeds germinate in copious numbers on bare ground in the autumn of their formation (Fig. 6.1), whilst others germinate in the following spring and summer (Butler, pers. comm.). It would seem therefore, that yarrow seedlings may establish with both autumn and spring-sown crops. Because autumn-germinated seedlings do not form rhizomes until the following spring (Fig. 6.1) they may be easily killed by cultivations in the autumn.

The observations on seed germination in this study indicated the existence of variable seed dormancy and that much seed germinates in the autumn following its formation. However, a planned investigation of seed and seedling ecology in the arable environment is most necessary if a more complete understanding of the ecology of yarrow is to be achieved. Specifically, a detailed study of the periodicity of germination in the field, the longevity of soil-borne seed and the status of seeds in the

establishment and spread of the plant in the rotations of the arable farming systems should hold high priority for future research on yarrow as on arable weed. With this knowledge, the planning of a long-term strategy for controlling yarrow will be able to be made on a more certain basis. The timing of cultivations or herbicide applications to kill seedlings could be more readily assessed, as could the need for suppression of seeding and the number of seasons for which this must be done to satisfactorily reduce, or eliminate the soil seed population.

6.3 COMPETITION

Several authors have suggested that yarrow is a poor competitor with dense, quick-growing crops and that the presence of such a crop may augment the debilitating effects of cultivations (Connell, 1930; Saxby, 1944; Hilgendorf and Calder, 1952). A crop of oats (*Avena sativa*) and tares (*Vicia sativa*) has been considered as a strong competitor with yarrow (Hilgendorf and Calder, 1952) while Mukula, Raatikainen, Lallukka and Raatikainen (1969) found yarrow was more abundant in oats and wheat (*Triticum aestivum*) than in barley (*Hordeum sativum*), indicating that barley may be the stronger competitor of these three cereal crops. Barley is commonly grown in the cereal districts of the South Island, where yarrow is a weed, and in Chapter 4, interference between the two species was quantitatively explored. The growth and reproductive potential of yarrow was markedly suppressed in the presence of barley but the barley was little affected by the yarrow. Rhizome dry matter production was greatly reduced (Fig. 4.11), through a reduction in initiation (Fig. 4.14) and elongation (Fig. 4.15), and seed production was markedly suppressed as a result of many plants remaining as vegetative rosettes (Fig. 4.17). Yarrow appeared to be a poor competitor with the barley because of its slower initial growth rate (Fig. 4.3), despite having emerged before the barley. The relative times of emergence of barley and yarrow is probably an important factor in the competitiveness of yarrow as Bourdôt and Butler (unpublished) found neither rhizomes nor flower stems were formed in a barley crop by yarrow plants which had emerged later than the barley.

Crops of low stature and/or those which have widely spaced plants, and are slow to form a canopy, have been observed to be poor competitors with yarrow, for example, white clover (*Trifolium repens*), peas (*Pisum*

sativum), beans (*Phaseolus vulgaris*) and, beets (*Beta vulgaris*) (Bourdôt, White and Field, 1979). These crops should be avoided in preference to barley or similarly competitive crops until yarrow is reduced sufficiently to prevent interference with susceptible crops. It is concluded that the growth and reproduction of yarrow can be greatly affected by the choice of crop, and that crop competition can play an important role in curtailing the spread of a yarrow population during the summer period by preventing or reducing seeding and rhizome formation which occur at this time of year (Fig. 6.1).

The competition study presented in Chapter 4 of this thesis, demonstrated clearly the marked ability of a barley crop to compete with and suppress a low population of yarrow regenerating rhizome fragments planted at 56 kg of rhizome dry matter ha^{-1}. This result indicated the utility of quick-growing, spring sown cereals like barley for control of the growth and development of yarrow during the summer. Furthermore, Bourdôt and Butler (unpublished) showed that the regrowing plants from up to 5210 kg rhizome dry matter ha^{-1} produced few new rhizomes and no flower stems during the presence of spring barley, indicating that populations arising from dense rhizome infestations may be greatly suppressed by barley. However the yield of the barley with 5210 kg rhizome dry matter ha^{-1} was 28% less than the yield with 740 kg ha^{-1}, suggesting yarrow competed strongly with this barley crop. The nature of this competition was not established but there was some indication that immobilisation of nitrogen in decaying rhizomes may have played some part in the effect. The barley plants on treatments where large amounts of rhizome had been incorporated into the soil immediately prior to sowing, showed visual symptoms of nitrogen deficiency. Allelopathy may also have played a role in reducing the barley yield for it is possible that substances released from yarrow, which have been shown to reduce the germination of some grasses (Scott, 1975), may be able to interfere with the growth of barley. It seemed unlikely that the regenerating yarrow competed with the barley for light, or indeed, water or nutrients because it remained as small rosettes throughout the growth of the barley. Other references to yarrow growing so densely as to 'choke out' cereal crops (Hilgendorf and Calder, 1952) suggest competition for light, or other

growth factors may occur when yarrow forms considerable aerial growth. It appears therefore, that yarrow may interfere with a cereal, or other crop by either competing directly for light, water or nutrients, or indirectly, by processes occurring during the decay of rhizome tissue in the soil.

In the light of these observations, it is suggested that further research into the nature of interference between yarrow and crop plants, especially the effect of decaying rhizomes, would be usefully carried out. The knowledge derived from such studies would be of considerable importance in determining the timing of control operations to reduce the amount of rhizome in the soil.

Yarrow not only survives and increases during the cropping phase of arable rotations, but also is frequently found as a component of pastures (Fuellman and Graber, 1938; Clapham, Tutin and Warburg, 1962; Deschenes, 1974; Matthews, 1975; Robocker, 1977). Its ability to establish and survive in this habitat has been partly explained by a capacity to tolerate reduced light intensities and to avoid shade by leaf extension (Fenner, 1978). In order to define the mechanism of this tolerance, a growth analysis study was carried out (Chapter 3). The results of this experiment confirmed that yarrow does indeed have a considerable capacity to tolerate shade. Adaptations of both the specific leaf area (Fig. 3.17), and the leaf weight ratio (Fig. 3.18), fully compensated for the decline in the net assimilation rate down to 40% full daylight (Fig. 3.23), allowing the plant to continue growing at the same rate as in full daylight. Almost complete compensation occurred to very low intensities, for at 20% full daylight, the relative growth rate had fallen to only 90% of its maximum. Furthermore, the results also demonstrated the remarkable plasticity of the leaves in response to shading. As shading became more intense, the leaves grew more nearly vertical and increased substantially in length (Fig. 3.5). Both of these responses would seem to be adaptations which could assist survival in communities of tall-growing species.

The compensation point for light was estimated to be approximately 3.6% full daylight (Fig. 3.23) which is less than the lowest levels commonly reached in pastures (Stern and Donald, 1962) and in cereals and other crops (Bula, Smith and Miller, 1954 ; Klebesadel and Smith, 1959;

Skuterud, 1977). This indicates that yarrow rosettes would be able to continue making positive growth in many pasture and crop environments and it is suggested that the low compensation point (cf., estimates for other species by Blackman and Wilson, 1951 a) may be an important attribute allowing survival in the crops and pastures of arable rotations. Even if light levels beneath a crop canopy were to fall below the compensation point of yarrow, the presence of food reserves in the rhizomes may carry a population over until the return of more favourable light conditions. On a similarly speculative note, it is suggested that seedlings prior to the development of rhizomes, may be less tenacious under conditions below the compensation point for light.

6.4 YARROW, A WEED OF ARABLE LAND?

A number of authors have made statements pertaining to the severity of detrimental effects caused by yarrow (see Section 1.4.1), but data supporting these assertions is wanting. Apart from the work of Bourdôt (unpublished) which demonstrated a reduction in the yield of a white clover seed crop of 46% in the presence of 104 yarrow flower stems m^{-2}, and that of Bourdôt and Butler (unpublished) showing a 28% yield reduction in barley when 5210 kg of rhizome dry matter ha^{-1} was present, there is no quantitative information on the yield reductions likely to be caused by yarrow populations in arable crops in New Zealand. Furthermore the distribution of the plant and the extent of the weed problem has not been reported. Thus, an economic assessment of the plant's weed status in New Zealand is not possible at present. Investigations of these aspects must hold some priority in future research on the biology of yarrow as a weed of arable land.

CONCLUSIONS

The following are the major conclusions drawn from the study on yarrow that is detailed in this thesis.

1. The success of yarrow as a weed of arable land is dependent to a large extent on the formation of rhizomes which exhibit an exceedingly strong apical dominance. This results in an accumulation of a store of dormant buds in an undisturbed environment. Upon fragmentation, only a proportion of the buds on the pieces form aerial shoots, apparently owing to the rapid re-establishment of a correlative mechanism amongst the buds, facilitating regeneration after successive cultivations.

Yarrow may also produce large numbers of highly viable seed, but the importance of this method of reproduction is uncertain, although apparently considerable.

2. The marked autumn and winter activity of rhizome growth is considered to be an exceptionally important characteristic, for it confers the advantage of allowing an increase in the plant's regenerative ability and occupation of the habitat during a period when many potential competitors are relatively dormant, for example, grasses and clovers, or absent such as in the undisturbed stubble of a summer-harvested cereal crop.

3. Insufficient information on the biology of yarrow is available to provide a basis for formulating a long-term strategy for reducing populations on arable land and suggestions for further research have been made in the previous discussion. Nevertheless, the studies presented in this thesis, in conjunction with results of other research, have revealed some aspects of the biology of yarrow which are relevant to its control.

Severe fragmentation of the rhizomes, followed at intervals not greater than the time required for new rhizomes to be formed, with subsequent disturbances to break off the previously formed shoots should lead to a marked reduction in the numbers of buds present in the soil. If new rhizomes were to be allowed to form between successive cultivations, an increase in the number of plants would most surely occur. Cultivations repeated at intervals allowing new rhizome growth, probably account for observations of increases in populations on land under cultivation.

An opportune time to implement such cultivations would be during the autumn, following the harvest of a summer crop, for disruption of rhizomes at this time would also prevent the autumn/winter build-up in rhizome reserves and buds. Autumn cultivations would also be likely to kill many seedlings, which germinate at this time of year, before they become more difficult-to-control rhizome-bearing plants. However, the seed germinates best on the soil surface (Yaskonis and Bandzaitene, 1970; Sowden, 1978), but becomes dormant when buried to only shallow depths (Kannangara, pers. comm.). Therefore delaying the initial cultivation until the autumn flush of seedlings from newly fallen seed has occurred would be advantageous.

4. Spring-sown barley is a powerful competitor against yarrow regenerating from buried rhizome fragments as a result of its much faster early growth. A well-grown crop, sown immediately after the final cultivation of the seed-bed, to ensure the barley does not emerge later than the yarrow, can completely suppress seeding and rhizome formation. However, crop yield reductions may be substantial if large amounts of rhizome are incorporated immediately prior to sowing the crop. Other rapid-growing spring-sown cereals are likely to be as equally competitive as barley. These crops are to be preferred to the less competitive crops such as white clover and peas until the yarrow population has been considerably reduced.

5. Cultivations during the autumn to exhaust rhizome reserves, prevent cool-season rhizome growth and to kill autumn-germinating seedlings, in combination with competitive spring-sown crops to limit rhizome and seed production during the summer is suggested as a strategy to reduce yarrow populations on arable land.

6. The compensation point for light appears to be very low (3 - 4% full daylight) making it possible for the plant to continue positive growth even under the most dense crop canopy.

Yarrow is not a high-light requiring species for it is able to compensate for reduced net assimilation rate in shaded conditions, by increasing the specific leaf area and leaf weight ratio. This tolerance of shade, augmented by plasticity of leaf length, are probably important features for survival of the plant in association with tall-growing species.

'The Song of

the Yarrow Fairy'

Among the harebells and the grass,
The grass all feathery with seed,
I dream, and see the people pass:
They pay me little heed.

And yet the children (so I think)
In spite of other flowers more dear,
Would miss my clusters white and pink,
If I should disappear.

APPENDICES

Appendix I Procedures for Growth Analysis

The Growth Analysis Relationships:

Techniques used to quantify the components of growth are collectively known as 'growth analysis'. The attributes of growth of individual plants and populations studied in Chapter 3 and 4 are:

the relative growth rate $(RGR_W) = \frac{1}{W} \cdot \frac{dW}{dt}$

the leaf area ratio $(LAR) = \frac{A}{W}$

the net assimilation rate $(NAR) = \frac{1}{A} \cdot \frac{dw}{dt}$ where W is total dry weight and A is leaf area.

These attributes are interrelated as:

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

The leaf area ratio was broken down into its components:

the specific leaf area $(SLA) = \frac{A}{LW}$

the leaf weight ratio $(LWR) = \frac{LW}{W}$ where LW is the leaf weight.

which are interrelated as:

$$\frac{A}{W} = \frac{A}{LW} \times \frac{LW}{W}$$ (Radford, 1967).

The growth of individual organs of the plants was also studied:

the relative growth rate of root $(RGR_{RT}) = \frac{1}{RT} \cdot \frac{dRT}{dt}$

the relative growth rate of stem $(RGR_S) = \frac{1}{S} \cdot \frac{dS}{dt}$

the relative growth rate of rhizome $(RGR_R) = \frac{1}{R} \cdot \frac{dR}{dt}$

the relative growth rate of leaf area $(RGR_A) = \frac{1}{A} \cdot \frac{dA}{dt}$ where RT is root dry weight, S is stem dry weight, R is rhizome dry weight and A is leaf area.

The ratios between the dry weights of rhizomes, flower stems and total plant dry weight were studied:

the rhizome weight ratio $(RWR) = \frac{R}{W}$

the stem weight ratio $(SWR) = \frac{S}{W}$

The traditional approach to growth analysis was to calculate the mean values for the various attributes over a given time interval (Radford, 1967). The drawbacks of this approach have been outlined by Hughes and Freeman (1967). Radford (1967) notes that confusion among those involved in growth analysis has resulted from the necessary introduction of assumptions regarding complex physiological relationships, especially of A vs. W; the latter relationship must be known before the mean NAR can be calculated.

A new concept of growth analysis was evolved that uses regression procedures of which Kvet *et al.* (1971) provide a complete description. The principle involves the choice of a suitable mathematical function which adequately describes the changes with time in the primary data of dry weight and leaf area. This function is represented by a smooth curve, fitted to the primary data so that it approximates the real growth curve. Derived functions (RGR, NAR, LAR and other ratios) can be accurately deduced from these without necessitating additional assumptions (Radford, 1967). A comparison of the classical and regression approaches is given by Sivakumar and Shaw (1978), who concluded that the regression approach was superior, especially with regard to the estimation of NAR.

Polynomial regressions have been used by several workers (Hughes and Freeman, 1967; Nicholls and Calder, 1973; Sivakumar and Shaw, 1978) and found satisfactory to describe the relationships of A and W to time. It is this type of function which is used in the growth analysis reported in Chapters 3 and 4 of this Thesis. The derived equations in their simplest form are:

$$\log_e W = a_o + a_1 t^1 + a_2 t^2 \quad \ldots\ldots\ldots \quad a_p t^p$$

$$\log_e A = b_o + b_1 t^1 + b_2 t^2 \quad \ldots\ldots\ldots \quad b_q t^q$$

$$\log_e LW = C_o + C_1 t^1 + C_2 t^2 \quad \ldots\ldots\ldots \quad c_r t^r$$

$$\log_e S = d_o + d_1 t^1 + d_2 t^2 \quad \ldots\ldots\ldots \quad d_x t^x$$

$$\log_e R = e_o + e_1 t^1 + e_2 t^2 \quad \ldots\ldots\ldots \quad e_y f_t^y$$

$$\log_e RT = f_o + f_1 t^1 + f_2 t^2 \quad \ldots\ldots\ldots \quad f_z t^z$$

The RGRs were derived directly by differentiation of these regression equations for:

$$\frac{d(\log_e W)}{dt} = \frac{1}{W} \cdot \frac{dW}{dt}$$

and $$\frac{d(\log_e A)}{dt} = \frac{1}{A} \cdot \frac{dW}{dt}$$

and $$\frac{d(\log_e S)}{dt} = \frac{1}{S} \cdot \frac{dS}{dt}$$

and $$\frac{d(\log_e R)}{df_t} = \frac{1}{R} \cdot \frac{dR}{dt}$$

and $$\frac{d(\log_e RT)}{dt} = \frac{1}{RT} \cdot \frac{dRT}{df_t}$$

The various ratios between plant components were derived as follows:

$$\frac{A}{W} = \text{antilog}(\log_e A - \log_e W)$$

$$\frac{A}{LW} = \text{antilog}(\log_e A - \log_e LW)$$

$$\frac{LW}{W} = \text{antilog}(\log_e LW - \log_e W)$$

$$\frac{R}{W} = \text{antilog}(\log_e R - \log_e W)$$

$$\frac{S}{W} = \text{antilog}(\log_e S - \log_e W)$$

and the NAR was simply obtained by:

$$\frac{d(\log_e W)}{dt} \div \text{antilog}(\log_e A - \log_e W).$$

Choosing the appropriate polynomial regression

Analysis of variance of the orthogonal regression components was carried out on the relevant dry weight and leaf area data. In Chapter 3 these were the total dry weight plant^{-1}, dry weights of leaf, root and stem, and leaf area plant^{-1} (Appendix III). In Chapter 4, (4.3.2) the data analysed for yarrow were total dry weight m^{-2}, dry weights of leaf, rhizome and stem m^{-2} and leaf area m^{-2} (Appendix V), and for barley, total dry weight and leaf weight m^{-2}, and leaf area m^{-2} (Appendix VIII). In (4.3.3) of Chapter 4, total dry weight, leaf weight, rhizome weight and leaf area m^{-2} were analysed (Appendix XI).

The regression equations were chosen so that they included terms up to the highest component declared significant, for components of time and the interaction of time with the factor of prime interest. For example, in Appendix VII, a cubic equation was fitted to the $\log_e$ (yarrow dry weights) for each level of the barley factor. A cubic was chosen because the cubic component of the barley x time interaction was significant at the 5% level, regardless of the fact that the cubic component of time was not significant.

It may be argued that fitting polynomials of the same order for all factor levels on the basis described above, constitutes overfitting for some of the factor levels (see Nicholls and Calder 1972 for discussion on this point). The alternative is to fit up to the highest component declared significant for each factor level independently. In the example just quoted the cubic coefficients were - .000014843, + .000003246 and + .000006103 for the three barley factor levels. These coefficients were known to vary significantly because the barley x time cubic component was significant. However, if the polynomials were fitted independently for each barley level, the coefficients would have become - .000014843, 0 and 0 since only the first coefficient was significantly different from zero. It was felt that this would not provide as fair a comparison between levels of the barley factor, as would leaving the coefficients at - .000014843, + .000003246 and + .000006103.

In the case discussed, any "overfitting" would involve just one extra component. The other cases which could be in debate are $\log_e A$ (Appendix VII), $\log_e W$ (Appendix X), $\log_e W$ (Appendix XIII) and $\log_e RT$ (Appendix IV). The first three of these cases would also involve the fitting of just one extra component, whilst the last case would involve two extra components.

Appendix II — Clarification of Statistical Procedures

The following procedures are based on those given in the statistical appendix addended to the growth analysis computer program written by Hughes and Freeman (1967). This appendix was kindly supplied to me by A.O. Nicholls, CSIRO, Australia and describes the fitting of cubics to both $\log_e W$ and $\log_e A$. The procedures were generalised by Mr D.J. Saville, M.A.F., Lincoln, to allow polynomials of higher order to be fitted to the data, and to enable the variance of various derived ratios and NAR to be calculated when the original growth curves eg. $\log_e A$ and $\log_e W$ were described by polynomials of different orders of complexity. To illustrate this generalisation, the fitted equations are given for the first level of the yarrow factor (no yarrow) in Appendix X. In this case, a cubic is fitted to $\log_e W$ and a quadratic to $\log_e A$.

1. Fitting the growth curves

Plant samples, having dry weights $W_1, W_2 \ldots\ldots W_n$, were taken at times $t_1, t_2 \ldots\ldots t_n$, where n is the number of observations (in this example n = 4 harvests x 6 replicates x 2 levels of barley = 48 for each level of the barley factor). A cubic regression equation of $\log_e W$ against t was fitted. At each time of harvesting, the observed value of $\log_e W$ is given by:

$$\log_e W = a + bt + ct^2 + dt^3 + \varepsilon$$

$$= -12.263 + 0.56566t - 0.0059364t^2 + 0.000021796t^3 \qquad (1)$$

where the first four terms represent the "true" curve and ε represents the error of observation. These errors are assumed to be independently normally distributed with mean 0 and the same variance σ^2.

It is convenient to write the equation as:

$$\log_e W = a_1 + b_1(\text{lin}) + C_1(\text{quad}) + d_1(\text{cub}) + \varepsilon$$

$$= 5.038 + 0.07545(\text{lin}) - 0.00152(\text{quad}) + 0.000021796(\text{cub}) \qquad (2)$$

where

const	=	1	const	=	1
lin	=	$t + A$	lin	=	$t - 67.5$
quad	=	$t^2 + Bt + C$	quad	=	$t^2 - 135.0t + 4195.0$
cub	=	$t^3 + Dt^2 + Et + F$	cub	=	$t^3 - 202.0t^2 + 13076.3t - 267556.5$

and

$$A = -\frac{\Sigma\left[(\text{const})t\right]}{\Sigma(\text{const})} = -67.5$$

$$B = -\frac{\Sigma(\text{lin})t^2}{\Sigma(\text{lin})t} = -135.0$$

$$C = -\frac{\Sigma\left[(\text{const})t^2\right] + B\Sigma\left[(\text{const})t\right]}{\Sigma(\text{const})} = 4195.0$$

$$D = -\frac{\Sigma(\text{quad})t^3}{\Sigma(\text{quad})t^2} = -202.5$$

$$E = -\frac{\Sigma\left[(\text{lin})t^3\right] + D\Sigma\left[(\text{lin})t^2\right]}{\Sigma\left|(\text{lin})t\right|} = 13076.3$$

$$F = -\frac{\Sigma(\text{const})t^3 + D\Sigma(\text{const})t^2 + E\Sigma(\text{const})t}{\Sigma(\text{const})} = -267556.5$$

The coefficients a_1 b_1 c_1 and d_1 are estimated by "least squares", i.e. are chosen to make the sum of the squares of the discrepancies between observed and fitted values as small as possible giving:

$$\hat{a}_1 = \frac{1}{n}\Sigma(\log_e W) \qquad \frac{\sigma^2}{n}$$

$$\hat{b}_1 = \frac{\Sigma(\text{lin})(\log_e W)}{\Sigma(\text{lin})^2} \qquad \frac{\sigma^2}{\Sigma(\text{lin})^2}$$

with variances (3)

$$\hat{c}_1 = \frac{\Sigma(\text{quad})(\log_e W)}{\Sigma(\text{quad})^2} \qquad \frac{\sigma^2}{\Sigma(\text{quad})^2}$$

$$\hat{d}_1 = \frac{\Sigma(\text{cub})(\log_e W)}{\Sigma(\text{cub})^2} \qquad \frac{\sigma^2}{\Sigma(\text{cub})^2}$$

Note: In these and following expressions the summation is over all the data values. This is n = 4 harvests x 6 replicates x 2 levels of barley = 48 for each level of the yarrow factor.

The same procedure is followed for fitting the quadratic equation to $\log_e A$, but excluding the calculation of $\hat{d}_1$ and (cub). The fitted quadratic equation for $\log_e A$ in the example was:

$$\log_e A = a + bt + ct^2 + \varepsilon$$

$$= -2.364 + 0.34746t - 0.0025057t^2$$

and can be expressed as:

$$\log_e A = a_1 + b_1(\text{lin}) + c_1(\text{quad}) + \varepsilon \qquad (4)$$

$$= 8.768 + 0.00919(\text{lin}) - 0.0025057(\text{quad})$$

The error variance for $\log_e W$ (σ_w^2) was estimated by:

$$\sigma_w^2 = \text{error mean square} = \frac{5.4759}{90} = 0.0608$$

The error variance for $\log_e A$(σ_A^2) was estimated by including the sums of squares due to the cubic components into the error sums of squares and dividing by the revised degrees of freedom.

$$\sigma_A^2 = \text{error mean square} = \frac{0.3161 + 0.4764 + 0.0066 + 0.0570 + 7.7537}{96} = .0897$$

From equation (2) the variance of a particular fitted value of $\log_e W$ is:

$$\sigma_w^2 \left[\frac{1}{n} + \frac{(\text{lin})^2}{\Sigma(\text{lin})^2} + \frac{(\text{quad})^2}{\Sigma(\text{quad})^2} + \frac{(\text{cub})^2}{\Sigma(\text{cub})^2} \right] \qquad (5)$$

Replacing σ_w^2 by its estimate and taking the square root gives the standard errors of the fitted values of $\log_e W$.

From equation (4) the variance of a particular fitted value of $\log_e A$ is:

$$\sigma_A^2 \left[\frac{1}{n} + \frac{(lin)^2}{\Sigma(lin)^2} + \frac{(quad)^2}{\Sigma(quad)^2} \right] \qquad (6)$$

Replacing σ_A^2 by its estimate and taking the square root gives the standard errors of the fitted value of $\log_e A$.

The same considerations apply to fitting curves of various degrees of complexity to other weight and area data.

2. Confidence limits

The type of confidence interval presented for the growth analysis is for any fixed value of t, the interval such that if it were calculated for each of an indefinitely long series of identical experiments, it would include the point on the "true" curve at that value of t on 95% of the occasions.

This was obtained by multiplying the standard error of the fitted value at that time by the two-sided 5% significant level of Students t distribution with error degrees of freedom ($t_{90}(.05)$ for $\log_e W$ and $t_{96}(.05)$ for $\log_e A$). As the number of observations n increases, the confidence limits will narrow, because the standard error decreases (since the factor in square brackets in (5) and (6) must decrease) and because the value of t decreases towards its limit of 1.96.

3. Derived functions of the fitted curves

(a) Relative growth rate (RGR) $= \frac{1}{W} \cdot \frac{dW}{dt} = \frac{d(\log_e W)}{dt}$

$$= \frac{d(a_1 + b_1(lin) + c_1(quad) + d_1(cub))}{dt}$$

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

The variance of a fitted value is:

$$\sigma_W^2 \left[\frac{1}{\Sigma(lin)^2} + \frac{(2t + B)^2}{\Sigma(quad)^2} + \frac{(3t^2 + 2Dt + E)^2}{\Sigma(cub)^2} \right] \qquad (7)$$

and standard errors and confidence limits are constructed as described above.

Identical considerations apply when curves of various degrees of complexity are fitted to other dry weight and area data and it is desired to derive the relative growth rates of these components.

(b) Leaf area ratio (LAR) $\frac{A}{W} = \text{antilog}(\log_e A - \log_e W)$

The variance of a fitted value of $(\log_e A - \log_e W)$ when a cubic regression has been fitted to $\log_e W$ and a quadratic to $\log_e A$ is:

$$\sigma_W^2 \left[\frac{1}{n} + \frac{(lin)^2}{\Sigma(lin)^2} + \frac{(quad)^2}{\Sigma(quad)^2} + \frac{(cub)^2}{\Sigma(cub)^2} \right]$$

$$+ (\sigma_A^2 - 2c) \left[\frac{1}{n} + \frac{(lin)^2}{\Sigma(lin)^2} + \frac{(quad)^2}{\Sigma(quad)^2} \right] \qquad (8)$$

where C is the covariance of the measurements of $\log_e W$ and $\log_e A$, estimated by $\hat{C}$, the residual sum of products in the analysis of variance divided by the error degrees of freedom. Normally C is positive. In the example, C = 0.06025.

Note: In (8), the σ_W^2 term and the σ_A^2 term include terms up to the highest order fitted to $\log_e W$ and $\log_e A$ respectively. The grouping of σ_A^2 and C in $(\sigma_A^2 - 2c)$ only applies if more terms are fitted with $\log_e W$ than $\log_e A$. If more terms were fitted to $\log_e A$ than $\log_e W$, C would be grouped with σ_W^2 as $(\sigma_W^2 - 2C)$.

The same procedure is followed when other ratios are calculated, by substituting the relevant components for $\log_e W$ and $\log_e A$.

(c) Net assimilation rate (NAR) $= \frac{1}{A} \cdot \frac{dW}{dt} = \frac{1}{W} \cdot \frac{dW}{dt} \div \frac{A}{W} =$ RGR $\div$ LAR

The variance of a fitted value of NAR when a cubic regression is fitted to $\log_e W$ and a quadratic to $\log_e A$ is:

$$\frac{\text{variance(fitted RGR)}}{(\text{fitted LAR})^2} + (\text{fitted RGR})^2 \text{ variance(fitted LAR)}$$

$$- 2 \frac{\text{fitted RGR}}{\text{fitted LAR}} \text{ Cov(fitted RGR, fitted LAR)}$$

where

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

$$= \sigma_W^2(\text{fitted LAR}) \left(\frac{\text{lin}}{\Sigma(\text{lin})^2} + \frac{\text{quad}(2t+B)}{\Sigma(\text{quad})^2} + \frac{\text{cub}(3t^2+2Dt+E)}{\Sigma(\text{cub})^2} \right)$$

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

The standard errors and confidence limits of the fitted values of NAR were constructed as previously shown.

Note: The expression multiplied by σ_W^2 has terms up to the highest order of the $\log_e W$ fit, and the expression multiplied by C has terms up to the highest order which appear in both the $\log_e A$ and the $\log_e W$ fit.

Appendix III The observed means of the logarithms of A, LW, W, RT, and S for the shading experiment (Chapter 3).

Transmitted P.A.R. as % of full daylight	Date of harvest (with days after imposition of shading treatments in parenthesis)					
	12 Jan. (7)	18 Jan. (13)	22 Jan. (17)	26 Jan. (21)	30 Jan. (25)	3 Feb. (29)
	Leaf area (A)					
100.0	4.873	5.430	5.671	5.941	6.197	6.573
46.8	5.005	5.549	5.874	6.250	6.401	6.697
23.7	4.945	5.490	5.804	6.128	6.419	6.650
6.4	4.744	5.016	5.249	5.414	5.635	5.872
	Leaf weight (LW)					
100.0	-0.194	0.608	0.870	1.148	1.461	1.768
46.8	-0.285	0.405	0.725	1.149	1.357	1.639
23.7	-0.484	0.141	0.417	0.772	1.110	1.351
6.4	-0.829	-0.532	-0.304	-0.158	0.091	0.312
	Total weight (W)					
100.0	0.395	1.158	1.496	1.793	2.093	2.398
46.8	0.215	0.884	1.252	1.677	1.909	2.164
23.7	-0.050	0.538	0.856	1.208	1.546	1.831
6.4	-0.378	-0.233	0.043	0.159	0.354	0.592
	Root weight (RT)					
100.0	-0.586	0.096	0.464	0.699	1.034	1.151
46.8	-0.915	-0.328	0.087	0.420	0.712	0.903
23.7	-1.309	-0.839	-0.483	-0.159	0.064	0.386
6.4	-1.546	-1.788	-1.427	-1.423	-1.473	-1.222
	Stem weight (S)					
100.0	-2.957	-2.149	-1.334	-1.092	-0.759	0.071
46.8	-2.916	-2.288	-1.612	-0.967	-0.913	-0.661
23.7	-3.456	-2.679	-2.021	-1.543	-1.324	-0.573
6.4	-3.796	-3.792	-3.131	-2.821	-2.704	-2.250

Values are the observed means of the logarithms ($\log_e$) of 6 2-plant replicates. Original values for LW, W, RT and S were g dry matter plant^{-1} and for A, cm^2 plant^{-1}.

Appendix IV Analysis of variance of orthogonal regression components for the shading experiment (Chapter 3).

Source	d.f.	$\log_e W$	$\log_e A$	$\log_e LW$	$\log_e RT$	$\log_e S$
Time	5	45.9956***	37.9597***	45.9681***	32.2177***	95.3038***
linear	1	45.7877***	37.8650***	45.6247***	31.9041***	93.6540***
quadratic	1	0.2028**	(0.0707) n.s.	0.2802**	0.1683*	0.1708 n.s.
cubic	1	(0.0036) n.s.	(0.0127) n.s.	(0.0394) n.s.	0.0241 n.s.	0.0114 n.s.
quartic	1	(0.0012) n.s.	(0.0040) n.s.	(0.0185) n.s.	0.1037 n.s.	1.4658***
quintic	1	(0.0002) n.s.	(0.0074) n.s.	(0.0053) n.s.	(0.0176) n.s.	(0.0018) n.s.
Light x Time	15	3.0920***	1.1166**	1.9466***	6.7825***	5.3821***
linear	3	2.7156***	0.9366***	1.6628***	5.9693***	3.8551***
quadratic	3	0.2678**	(0.0922) n.s.	0.1620 n.s.	0.4787***	0.6243 n.s.
cubic	3	(0.0447) n.s.	(0.0458) n.s.	(0.0607) n.s.	0.0240 n.s.	0.7023 n.s.
quartic	3	(0.0311) n.s.	(0.0157) n.s.	(0.0224) n.s.	0.2867*	0.0390 n.s.
quintic	3	(0.0327) n.s.	(0.0263) n.s.	(0.0387) n.s.	(0.0237) n.s.	(0.1615) n.s.
Error	100	1.9133	3.1051	2.5829	3.2619	10.1341

In this and succeeding anova tables; (i) The values are sums of squares; (ii) Probabilities were tested against the error variance with appropriate degrees of freedom; *** = $P \leq .001$; ** = $.001 < P \leq .01$; * = $.01 < P \leq .05$; n.s. = $.05 < P$; (iii) Terms which were subsequently pooled with the error term are enclosed in brackets.

Appendix V The observed means of the logarithms of W, A, LW, R, and S of yarrow on the five harvest occasions, averaged over both yarrow densities, for the yarrow/barley experiment (Chapter 4).

Barley density (plants m^{-2})	Date of harvest (with days after planting rhizome fragments in parenthesis)				
	17 Dec. (42)	3 Jan. (59)	20 Jan. (76)	6 Feb. (93)	23 Feb. (110)
	Total weight (W)				
0	1.967	3.146	4.643	5.802	6.404
194	1.730	2.847	3.474	3.855	3.937
359	1.761	2.647	3.083	3.387	3.600
	Leaf area (A)				
0	5.339	7.065	8.673	9.810	9.755
194	5.068	6.783	7.612	7.932	7.637
359	5.117	6.500	7.014	7.336	7.255
	Leaf weight (LW)				
0	0.609	2.530	3.901	4.912	5.045
194	0.140	2.159	2.854	3.085	2.909
359	0.184	1.903	2.278	2.508	2.531
	Rhizome weight (R)				
0	a	0.054	2.010	3.664	4.277
194	a	-0.938	0.097	0.972	0.997
359	a	-1.541	-0.853	-0.445	0.171
	Stem weight (S)				
0	b	1.118	2.641	4.589	5.378
194	b	0.958	1.564	2.285	2.574
359	b	0.730	1.212	1.856	2.209

Values are the observed means of the logarithms for both densities (25 and 50 10 cm - rhizome fragments m^{-2}) of yarrow and are therefore the means of 12 observations. Original values for W, LW, R and S were g dry matter m^{-2} and for A, cm^2 m^{-2}; a, rhizomes not formed; b, excluded from analysis.

Appendix VI Analysis of variance of yarrow averaged over all harvest occasions (main-plot analysis) for the yarrow/barley experiment (Chapter 4).

Source	d.f.	$\log_e W$	$\log_e A$	$\log_e LW$	$\log_e R$	$\log_e S$
Yarrow density	1	11.5979***	9.3911***	10.6814***	4.1200 n.s.	6.3294***
Barley density	2	76.2489***	71.8762***	75.9459***	253.7855***	101.7459***
Yarrow x Barley	2	0.3139 n.s.	1.3459 n.s.	0.8638 n.s.	3.3141 n.s.	0.4008 n.s.
Replicates	5	2.1108	4.0634	3.3391	12.9605	5.3442
Error	25	5.6910	6.8031	7.5617	32.2428	9.0636

Appendix VII Analysis of variance of orthogonal regression components for yarrow (sub-plot analysis) in yarrow/barley experiment (Chapter 4).

Source	d.f.	$\log_e W$	$\log_e A$	$\log_e LW$	d.f.	$\log_e R$	$\log_e S$
Time	4	190.6991***	250.3785***	256.9436***	3	146.9949***	131.5155***
linear	1	182.6732***	211.1812***	211.9030***	1	140.9429***	128.7920***
quadratic	1	7.9829***	38.9789***	43.4077***	1	5.8758**	1.3917*
cubic	1	0.0420 n.s.	0.0452 n.s.	1.1938*	1	(0.1762) n.s.	1.3318*
quartic	1	(0.0010) n.s.	(0.1732) n.s.	(0.4391) n.s.	n.a.	n.a.	n.a.
Yarrow x Time	4	1.0939 n.s.	0.5221 n.s.	0.8306 n.s.	3	1.3029 n.s.	1.4239 n.s.
linear	1	0.8885**	0.4773 n.s.	0.6971 n.s.	1	0.3107 n.s.	0.1767 n.s.
quadratic	1	0.0059 n.s.	0.1002 n.s.	0.0162 n.s.	1	0.2344 n.s.	0.1235 n.s.
cubic	1	0.0354 n.s.	0.0101 n.s.	0.0004 n.s.	1	(0.7578) n.s.	1.1237*
quartic	1	(0.1641) n.s.	(0.0247) n.s.	(0.1169) n.s.	n.a.	n.a.	n.a.
Barley x Time	8	37.1031***	31.0551***	26.1946***	6	30.5408***	36.4690***
linear	2	35.5721***	28.4633***	23.8878***	2	27.3546***	35.4229***
quadratic	2	0.3933 n.s.	0.8759 n.s.	0.7820 n.s.	2	2.6069 n.s.	0.5736 n.s.
cubic	2	1.0765*	1.6901*	1.4946*	2	(0.5793) n.s.	0.4725 n.s.
quartic	2	(0.0611) n.s.	(0.0258) n.s.	(0.0302) n.s.	n.a.	n.a.	n.a.
Yarrow x Barley x Time	8	0.7770 n.s.	1.9785 n.s.	1.3251 n.s.	6	0.9635 n.s.	1.2997 n.s.
linear	2	0.0366 n.s.	0.9226 n.s.	0.5673 n.s.	2	0.1916 n.s.	0.0223 n.s.
quadratic	2	0.2942 n.s.	0.0948 n.s.	0.0690 n.s.	2	0.1345 n.s.	0.9152 n.s.
cubic	2	0.3821 n.s.	0.8460 n.s.	0.5951 n.s.	2	(0.6374) n.s.	0.3622 n.s.
quartic	2	(0.0641) n.s.	(0.1151) n.s.	(0.0938) n.s.	n.a.	n.a.	n.a.
Error	120	16.4482	28.2164	26.8195	90	71.4122	24.7347

Appendix VIII The observed means of the logarithms of W, A, and LW of barley on the four harvest occasions, averaged over both barley densities, for the yarrow/barley experiment (Chapter 4).

Yarrow density (10 cm - rhizome) fragments m^{-2})	Date of harvest (with days after planting rhizome fragments in parenthesis) 17 Dec. (42)	3 Jan. (59)	20 Jan. (76)	6 Feb. (93)	23 Feb. (110)
	Total weight (W)				
0	2.638	4.923	6.006	6.531	b
25	2.500	4.421	5.897	6.504	b
50	2.479	4.655	5.692	6.427	b
	Leaf area (A)				
0	7.817	9.392	9.593	8.271	a
25	7.668	8.897	9.477	8.270	a
50	7.616	9.126	9.344	8.302	a
	Leaf weight (LW)				
0	2.441	4.349	4.245	3.203	b
25	2.298	3.891	4.157	3.219	b
50	2.284	4.133	4.036	3.216	b

Values are the observed means of the logarithms for both densities (194 and 359 plants m^{-2}) of barley and are therefore the means of 12 observations. Original values for W and LW were g dry-matter m^{-2} and for A, cm^2 m^{-2}; a, all green leaf tissue had senesced; b, excluded from analysis as assimilation had ceased.

Appendix IX Analysis of variance of barley averaged over all harvest occasions (main-plot analysis) for the yarrow/barley experiment (Chapter 4).

Source	d.f.	$\log_e W$	$\log_e A$	$\log_e LW$
Yarrow density	2	1.3218**	1.0535*	0.7844*
Barley density	1	3.7426***	2.2696***	1.6546***
Yarrow x Barley	2	0.0157 n.s.	0.0576 n.s.	0.0407 n.s.
Replicates	5	0.7935	1.1232	0.7122
Error	25	2.0488	3.1287	2.0545

Appendix X Analysis of variance of orthogonal regression components for barley (sub-plot analysis) in the yarrow/barley experiment (Chapter 4).

Source	d.f.	$\log_e W$	$\log_e A$	$\log_e LW$
Time	3	326.8850 ***	70.2307 ***	80.1153 ***
linear	1	306.2673 ***	7.7407 ***	12.5080 ***
quadratic	1	20.3957 ***	62.1740 ***	66.4374 ***
cubic	1	0.2220 n.s.	(0.3161) n.s.	1.1699 ***
Yarrow x Time	6	1.0500 *	1.0583 n.s.	0.9205 *
linear	2	0.1806 n.s.	0.2382 n.s.	0.2178 n.s.
quadratic	2	0.3167 n.s.	0.3436 n.s.	0.2740 n.s.
cubic	2	0.5524 *	(0.4764) n.s.	0.4287 *
Barley x Time	3	2.4824 ***	3.7232 ***	4.0972 ***
linear	1	2.2300 ***	3.5116 ***	3.7996 ***
quadratic	1	0.2515 *	0.2051 n.s.	0.2976 *
cubic	1	0.0010 n.s.	(0.0066) n.s.	0.0000 n.s.
Yarrow x Barley x Time	6	0.3380 n.s.	0.3179 n.s.	0.2782 n.s.
linear	2	0.2976 n.s.	0.2592 n.s.	0.2205 n.s.
quadratic	2	0.0087 n.s.	0.0017 n.s.	0.0071 n.s.
cubic	2	0.0316 n.s.	(0.0570) n.s.	0.0506 n.s.
Error	90	5.4759	7.7537	5.6495

Appendix XI The observed means of the logarithms of W, A, LW, and R of yarrow on the five harvest occasions, averaged over both densities of yarrow, during autumn and winter (Chapter 4).

Date of harvest (with days after planting rhizome fragments in parenthesis)

Density of previous barley crop (plants m^{-2})	29 March (144)	2 May (178)	2 July (239)	7 Aug. (275)	8 Sept. (307)
	Total weight (W)				
0	6.729	6.564	6.715	6.909	6.857
194	3.768	4.795	5.431	5.528	5.624
359	3.750	4.470	5.254	5.431	5.646
	Leaf area (A)				
0	9.553	9.500	8.862	8.884	8.830
194	7.329	8.725	8.710	8.178	8.211
359	7.489	8.385	8.501	8.298	8.164
	Leaf weight (LW)				
0	4.881	4.841	4.153	4.351	4.133
194	2.632	3.846	3.830	3.526	3.558
359	2.815	3.459	3.588	3.633	3.524
	Rhizome weight (R)				
0	4.708	5.274	6.069	6.354	6.104
194	2.097	3.831	4.972	5.233	5.357
359	1.636	3.543	4.810	5.081	5.377

Values are the observed means of the logarithms for both densities (25 and 50 cm-rhizome fragments) of yarrow; means of 12 observations. Original values for W, LW and R were g dry-matter m^{-2} and for A, cm^2 m^{-2}.

Appendix XII Analysis of variance of yarrow averaged over all harvest occasions during the autumn and winter (main-plot analysis), for the yarrow/barley experiment (Chapter 4).

Source	d.f.	$\log_e W$	$\log_e A$	$\log_e LW$	$\log_e R$
Yarrow density	1	2.2161 **	0.9747 n.s.	1.2292 n.s.	2.6521 **
Barley density	2	127.9177 ***	34.4985 ***	42.6620 ***	92.2813 ***
Yarrow x Barley	2	0.8055 n.s.	0.6936 n.s.	0.8129 n.s.	0.3270 n.s.
Replicates	5	1.5382	0.5433	0.7052	2.7815
Error	25	5.9699	11.7417	14.3172	8.8109

Appendix XIII - Analysis of variance of orthogonal regression components for yarrow (sub-plot analysis) during the autumn and winter for the yarrow/barley experiment (Chapter 4).

Source	d.f.	$\log_e$W	$\log_e$A	$\log_e$LW	$\log_e$R
Time	4	42.6678***	11.7582***	7.0830***	205.1213***
linear	1	39.8568***	0.0543 n.s.	0.4516 n.s.	180.4118***
quadratic	1	2.7182***	6.9389***	3.5484***	23.2117***
cubic	1	0.0924 n.s.	4.6824***	2.4325**	1.3841*
quartic	1	(0.0005) n.s.	(0.0825) n.s.	(0.6505) n.s.	(0.1137) n.s.
Yarrow x Time	4	0.6809 n.s.	1.3435 n.s.	1.8936 n.s.	0.3340 n.s.
linear	1	0.2947 n.s.	0.7359 n.s.	0.8664 n.s.	0.0102 n.s.
quadratic	1	0.0213 n.s.	0.3770 n.s.	0.5605 n.s.	0.1239 n.s.
cubic	1	0.1401 n.s.	0.0510 n.s.	0.0480 n.s.	0.1486 n.s.
quartic	1	(0.2250) n.s.	(0.1795) n.s.	(0.4187) n.s.	(0.0512) n.s.
Barley x Time	8	16.7764***	17.8267***	16.5318***	21.4423***
linear	2	13.2117***	9.4428***	10.7126***	17.5214***
quadratic	2	2.6328***	6.6337***	4.0741***	1.7049*
cubic	2	0.8875*	1.5087*	1.3591 n.s.	2.2036*
quartic	2	(0.0444) n.s.	(0.2416) n.s.	(0.3860) n.s.	(0.0124) n.s.
Yarrow x Barley x Time	8	1.1295 n.s.	0.8945 n.s.	1.2055 n.s.	3.1458 n.s.
linear	2	0.6276 n.s.	0.4854 n.s.	0.5616 n.s.	1.3005 n.s.
quadratic	2	0.1301 n.s.	0.0716 n.s.	0.1213 n.s.	0.9384 n.s.
cubic	2	0.2533 n.s.	0.1934 n.s.	0.3126 n.s.	0.5301 n.s.
quartic	2	(0.1185) n.s.	(0.1441) n.s.	(0.2101) n.s.	(0.3768) n.s.
Error	120	15.4186	24.9412	30.6553	27.8413

Appendix XIV Total length of rhizome (m m^{-2}) for the yarrow/barley experiment (Chapter 4).

Density of Yarrow (10 cm - rhizome fragments m^{-2})	Density of barley (plants m^{-2}) 0	194	359
	3 Jan.		
25	2.39	1.18	0.51
50	3.54	1.18	0.88

The S.E. (mean) was 0.434; interaction was n.s.

	20 Jan.		
25	8.58	2.83	1.07
50	19.33	3.48	2.56

The S.E. (mean) was 1.388; interaction was significant at 1% level.

	6 Feb.[a]					
25	7.89	(22.31)	6.07	(3.58)	4.88	(1.09)
50	8.58	(44.31)	6.19	(4.04)	5.01	(1.24)

The S.E. (mean) was 0.213; interaction was n.s.

	23 Feb.[a]					
25	8.36	(35.42)	5.77	(2.67)	5.10	(1.36)
50	8.65	(47.77)	5.78	(2.70)	5.50	(2.03)

The S.E. (mean) was 0.333; interaction was n.s.

a, analysis of variance was performed on $\log_e(X + 1.0)$ where x was the total length of rhizome in mm 0.12 m^{-2}. The backtransformed means are presented in brackets on a m m^{-2} basis.

Appendix XV Total number of rhizomes m^{-2} for the yarrow/barley experiment (Chapter 4).

Density of Yarrow (10 cm - rhizome fragments m^{-2})	Density of barley (plants m^{-2}) 0	194	359
	17 Dec.		
25	2	0	0
50	6	1	0
	3 Jan.		
25	92	60	38
50	146	50	53

The S.E. (mean) was 12.1; interaction was significant at 5% level.

	20 Jan.		
25	214	71	35
50	428	96	79

The S.E. (mean) was 27.4; interaction was significant at 0.1% level.

	6 Feb.		
25	390	81	48
50	761	121	58

The S.E. (mean) was 40.9; interaction was significant at 0.1% level.

	23 Feb.		
25	625	100	56
50	723	129	94

The S.E. (mean) was 44.3; interaction was n.s.

Appendix XVI Frequency tables for yarrow stem height, averaged over both yarrow densities for the yarrow/barley experiment (Chapter 4).

Height classes (mm)	Barley density (plants m^{-2}) 0		194		359	
	Number	%	Number	%	Number	%
	17 Dec.					
1 - 40	13	18	10	16	11	17
41 - 80	59	81	52	87	54	83
81 - 120	1	1	0	0	0	0
	73		62		65	
	3 Jan.					
1 - 40	10	13	11	13	5	7
41 - 80	60	78	72	85	71	93
81 - 120	9	11	2	2	0	0
	79		85		76	
	20 Jan.					
1 - 40	0	0	1	1	5	7
41 - 80	39	51	59	76	58	79
81 - 120	16	21	4	5	2	3
121 - 160	3	4	6	8	4	5
161 - 200	5	6	2	3	2	3
201 - 240	4	5	3	4	1	1
241 - 280	4	5	1	1	0	0
281 - 320	2	3	0	0	0	0
321 - 360	2	3	2	3	0	0
361 - 400	2	3	0	0	1	1
401 - 440	0	0	0	0	0	0
	77		78		73	
	6 Feb.					
1 - 40	0	0	5	6	6	8
41 - 80	7	9	49	63	46	65
81 - 120	4	5	2	3	4	6
121 - 160	1	1	3	4	1	1
161 - 200	3	4	0	0	1	1
201 - 240	1	1	2	3	1	1
241 - 280	1	1	0	0	0	0
281 - 320	4	5	0	0	1	1
321 - 360	5	7	2	3	2	3
361 - 400	6	8	2	3	0	0
401 - 440	12	16	1	1	2	3
441 - 480	17	23	4	5	3	4
481 - 520	11	15	2	3	1	1
521 - 560	2	3	5	6	3	4

Continued .../

Appendix XVI (Continued)

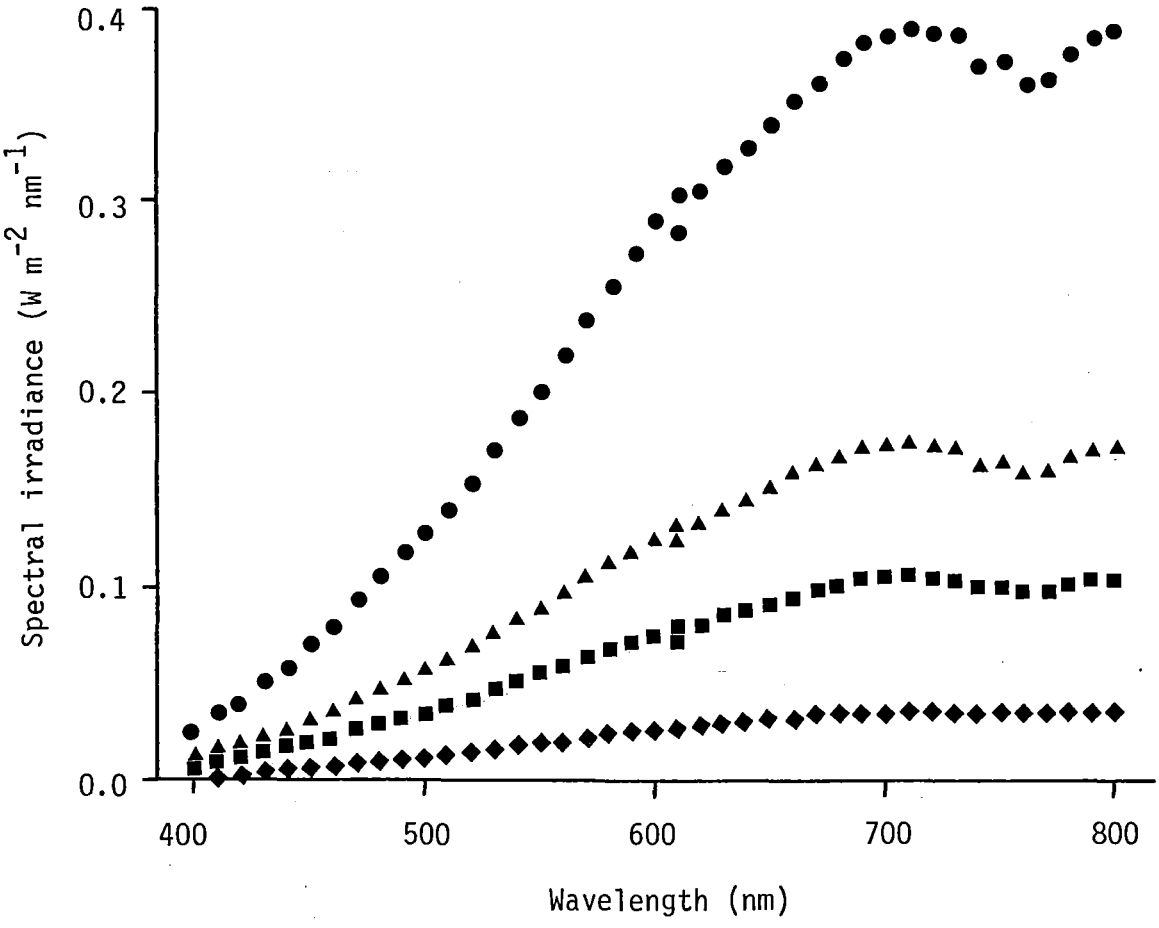
Height classes (mm)	0		194		359	
	Number	%	Number	%	Number	%
	6 Feb. (Cont.)					
561 - 600	0	0	1	1	0	0
601 - 640	0	0	0	0	0	0
641 - 680	0	0	0	0	0	0
	74		78		71	
	23 Feb.					
1 - 40	0	0	2	3	2	3
41 - 80	11	14	49	68	52	73
81 - 120	1	1	1	1	1	1
121 - 160	0	0	0	0	0	0
161 - 200	0	0	0	0	0	0
201 - 240	0	0	0	0	1	1
241 - 280	1	1	0	0	0	0
281 - 320	0	0	0	0	0	0
321 - 360	2	3	3	4	1	1
361 - 400	1	1	0	0	5	7
401 - 440	1	1	1	1	2	3
441 - 480	9	12	2	3	2	3
481 - 520	9	12	3	4	3	4
521 - 560	8	12	3	4	1	1
561 - 600	15	11	6	8	1	1
601 - 640	11	20	1	1	0	0
641 - 680	7	14	1	1	0	0
	76		72		71	

In the construction of these tables, the data was totalled over the 6 replicates and averaged over both densities of yarrow. The total at the bottom of the number column is the number of shoots 6 x .12 (.72) m^{-2}.

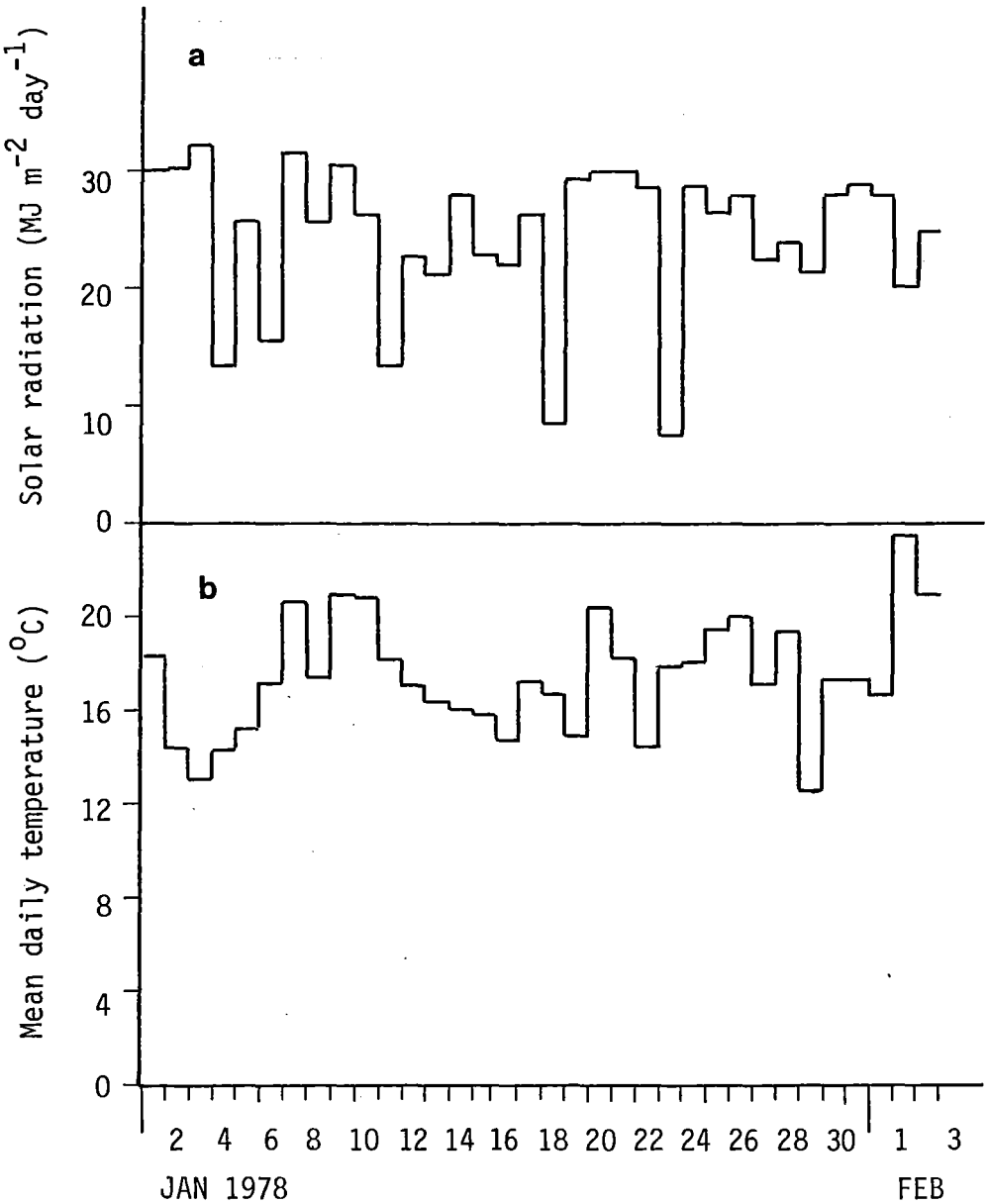
Appendix XVII Height of barley as affected by the density of yarrow and barley, and time in the yarrow/barley experiment (Chapter 4).

Density of barley (plants m^{-2})	Density of yarrow (10 cm - rhizome fragments m^{-2}) 0	25	50
	17 Dec.		
194	53	45	40
359	53	45	45
	The S.E. (mean) was 2.3; interaction was n.s.		
	3 Jan.		
194	129	117	116
359	146	127	124
	The S.E. (mean) was 7.1; interaction was n.s.		
	20 Jan.		
194	492	482	485
359	463	460	443
	The S.E. (mean) was 14.4; interaction was n.s.		
	6 Feb.		
194	534	504	500
359	485	484	466
	The S.E. (mean) was 12.7; interaction was n.s.		
	23 Feb.		
194	525	511	522
359	476	475	475
	The S.E. (mean) was 13.2; interaction was n.s.		

Values are heights (mm) from ground level to base of the youngest expanded leaf.



Appendix XVIII Spectral transmission of shade cloth used in the shading experiment (Chapter 3). ●, black box alone; ▲, 46.8% cloth; ■, 23.7% cloth; ◆, 6.4% cloth. Normalisation of the spectral irradiance to each treatment's 700 nm value, showed the spectral transmission of each cloth, within the wavelength range ofthe test, was the same.



Appendix XIX

Climatic data for the months of January and early February 1978. **a**, solar radiation (MJ M^{-2} day^{-1}) measured at Christchurch Airport, 15 km from the shading trial site; **b**, mean daily air temperature (^{o} C), recorded at the Lincoln College Meterological Station, derived as the mean of the daily minimums and maximums.

Appendix XX Rhizome Planting Device

In order to allow consistently accurate depth placement of rhizome fragments in the soil, a scissor-like device was constructed, which could plant a single fragment, up to 10 cm in length, at a time (Fig. XX.1). To plant a fragment, the device was simply loaded with the fragment when in the closed position (Fig. XX.2a), plunged into the soil to the required depth with the aid of the foot, and then opened by closing the handles, thus releasing the fragment (Fig. XX.2b). The depth to which the device moved into the soil was controlled by the attachment of a stop on either side (Figs. XX 2a, 2b), and when a certain density or spatial arrangement of rhizome fragments was required, this was achieved with the aid of a movable jig (Fig. XX.1). Further details of the construction of this device are available from Mr B.E. Smith, Plant Science Department, Lincoln College.

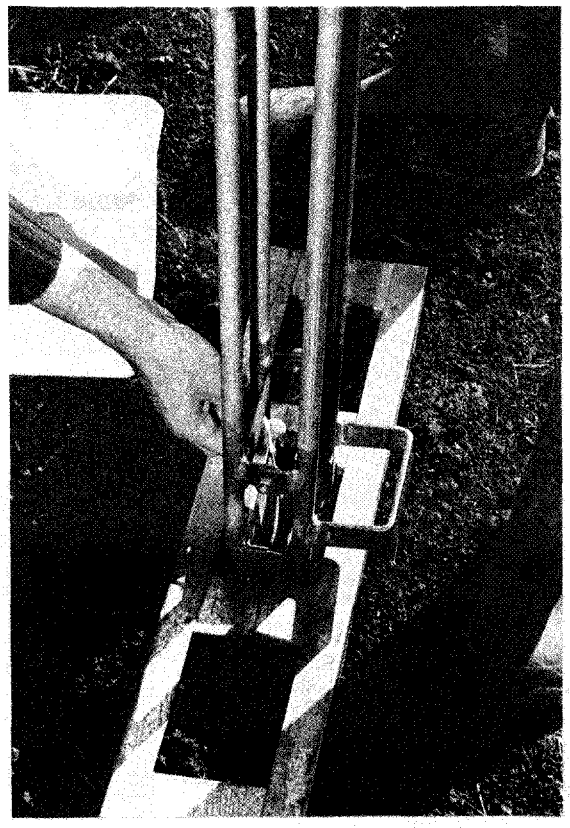


Figure XX.1 The rhizome planting device illustrating the method of loading and the jig which facilitated accurate spatial arrangement of the planted rhizome fragments.

Continued .../

Appendix XX (Continued)

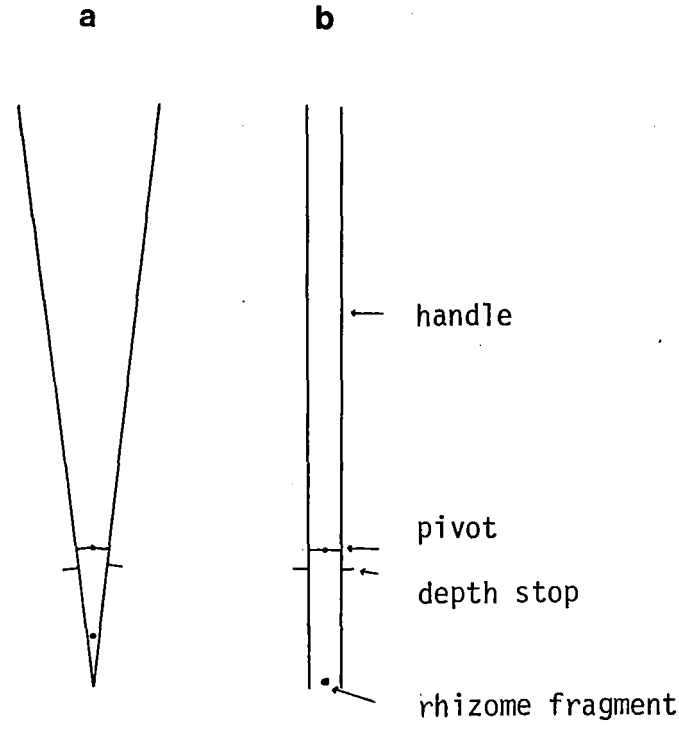


Figure XX.2 Schematic diagram of the planting device. **a**) in the closed position; **b**) in the open position.

Appendix XXI The mean dry weights of capitula and the ratio of capitula: total plant dry weight for harvest 5 (day 110) of the yarrow/barley experiment (Chapter 4).

yarrow density (10 cm rhizome fragments m^{-2})	barley density (plants m^{-2})	Capitulum dry weight (g m^{-2})	Ratio of capitulum: total dry weight
25	0	127.8	0.218
25	194	4.2	0.063
25	359	1.4	0.066
50	0	125.8	0.186
50	194	7.1	0.077
50	359	4.1	0.067
S.E. (mean)		10.61	0.0173
interaction		n.s.	n.s.

Values are the observed means of 6 replicates.

Appendix XXII Barley yield components (at 11.7% moisture) of the yarrow/barley experiment (Chapter 4).

barley density (plants m^{-2})	yarrow density (10 cm rhizome fragments m^{-2})	Yield kg ha^{-1}	Ears m^{-2}	Spikelets Ear^{-1}	Grains Ear^{-1}	1000 Grain Wt.
194	0	4630	682	25.0	21.6	41.9
194	25	4600	635	24.7	21.2	42.3
194	50	4100	644	23.4	19.5	42.9
359	0	4420	660	23.1	19.8	40.9
359	25	4510	668	22.9	19.7	41.8
359	50	4360	637	22.5	19.4	42.6
S.E. (mean)		208	31.3	.33	.43	.59
interaction		n.s.	n.s.	n.s.	n.s.	n.s.

Appendix XXIII Temperature recordings in the shade houses used in the shading experiment (Chapter 3). Values are daily maximums and minimums.

	Light intensity (% full daylight PAR)							
	100%		46.8%		23.7%		6.4%	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
17 January	23.0	6.5	20.0	7.0	20.0	7.5	20.0	8.0
18 January	30.0	13.0	28.0	13.5	28.0	14.0	27.5	13.5
19 January	24.0	8.0	21.0	8.0	21.5	9.0	21.0	9.0
Mean	25.7	9.2	23.0	9.5	23.2	10.2	22.8	10.2
mean difference between shade treatment and no shade			-2.7	+0.3	-2.5	+1.0	-2.9	+1.0

Appendix XXIV The observed means of the logarithms of the planted rhizome fragments on four harvest occasions, averaged over both yarrow densities, for the yarrow/barley experiment (Chapter 4).

barley density (plants m^{-2})	Date of harvest (with days after planting rhizome fragments in parenthesis).				
	17 Dec. (42)	3 Jan. (59)	20 Jan. (76)	6 Feb. (93)	23 Feb. (110)
0	a	1.701	2.049	2.599	2.840
194	a	1.633	1.850	1.965	2.060
359	a	1.572	1.787	1.942	1.948

Values are the observed means of the logarithms for both densities (25 and 50 10 cm rhizome fragments m^{-2}); means of 12 observations. Original values were g dry-matter m^{-2}; a, excluded from analysis.

Appendix XXV Analysis of variance of planted rhizome dry weight for the yarrow/barley experiment (Chapter 4).

Main-plot analysis

Source	d.f.	
Yarrow density	1	13.5616***
Barley density	2	6.6528***
Yarrow x Barley	2	0.3745 n.s.
Replicates	5	1.3211
Error	25	3.0278

Sub-plot analysis

Source	d.f.	
Time	3	9.0731***
linear	1	8.8265***
quadratic	1	0.1932 n.s.
cubic	1	0.0534 n.s.
Yarrow x Time	3	0.1104 n.s.
linear	1	0.0979 n.s.
quadratic	1	0.0050 n.s.
cubic	1	0.0075
Barley x Time	6	2.8911***
linear	2	2.7622***
quadratic	2	0.0181 n.s.
cubic	2	0.1107 n.s.
Yarrow x Barley x Time	6	1.1868*
linear	2	0.1109 n.s.
quadratic	2	0.5536*
cubic	2	0.6214*
Error	90	6.4533

Appendix XXVI Daily rainfall (mm) for the period: November 1978 to March 1979 inclusive. Recorded at the Lincoln College Meteorological Station.

Number of rhizomes plant^{-1}

Day	Nov.	Dec.	Jan.	Feb.	Mar.
1	2.7	1.0			
2		1.7			
3		0.2	10.4		
4	4.1		7.5		
5		0.3			
6		0.3			
7		1.1			0.1
8					
9				2.0	
10	0.3	29.2			7.4
11	11.2	7.8			0.2
12	8.1	43.9			
13		14.7	1.1		2.5
14	4.0	16.7		1.2	2.6
15	13.0	0.4	0.7		26.5
16					1.0
17		0.3			
18					
19				8.9	
20					27.9
21		27.8		14.3	33.9
22				4.3	3.4
23		3.8			
24	0.2				
25					6.8
26					
27			1.2	0.6	
28			0.3	16.3	8.6
29				-	4.5
30				-	7.5
31		-		-	-

Appendix XXVII Number and total length of rhizomes, total number of rhizome nodes (axillary buds) and percentage of total buds active per plant. Means and standard deviations are presented in Experiment 1, Chapter 5; R, rhizome propagated plants; S, seed propagated plants.

Number of rhizomes plant^{-1}

Individual	24 Jan.		11 Feb.		26 Feb.		27 March		17 April		19 June	
	R	S	R	S	R	S	R	S	R	S	R	S
1	0	0	6	0	17	33	54	82	45	30	79	71
2	0	1	9	10	14	33	44	51	46	44	76	165
3	0	2	16	13	15	38	38	18	77	82	97	84
4	3	2	5	16	21	42	43	37	59	112	69	96
5	6	0	12	13	10	8	42	29	54	23	64	58
6	3	8	18	17	20	16	55	57	61	10	94	132
7	0	0	5	7	30	12	46	10	45	22	90	78
8	0	0	14	4	15	9	33	14	35	97	61	67
9	2	2	13	6	33	22	47	6	41	16	67	54
10	0	0	3	12	21	11	11	2	77	12	73	56
11	1	5	10	5	27	15	21	15	56	109	65	122
12	4	1	6	8	18	4	29	11	43	44	55	17
$\bar{X}$	1.6	1.8	9.8	9.3	20.1	20.3	38.6	27.7	53.3	50.1	74.2	83.3
S.D.	2.02	2.45	4.86	5.14	6.87	12.99	13.10	24.50	13.51	39.01	13.18	40.22

Total length of rhizomes (m) plant^{-1}

1	0	0	.11	.026	1.191	1.231	4.759	4.528	7.842	2.414	12.8	6.33
2	0	.02	.215	.160	.599	.922	4.973	2.666	7.444	3.045	18.91	24.82
3	0	.022	.385	.210	.435	1.049	5.348	.734	9.641	4.610	13.32	8.11
4	.04	.025	.115	.484	.775	1.088	5.885	1.659	4.847	6.071	14.91	9.67
5	.06	0	.360	.320	.419	.262	4.952	3.338	9.877	.864	15.33	6.99
6	.018	.105	.432	.412	2.383	.420	6.891	3.775	8.190	.464	16.84	15.82
7	0	0	.062	.070	1.232	.276	4.319	.483	3.181	.597	12.42	16.17
8	0	0	.295	.045	.516	.318	5.238	2.104	4.361	5.932	13.28	5.69
9	.024	.02	.250	.070	1.850	.511	5.242	.260	4.888	.551	11.14	6.42
10	0	0	.045	.215	.890	.389	.418	1.999	6.189	.663	17.44	6.73
11	.007	.033	.187	.102	1.080	.192	1.482	.310	7.202	7.216	18.52	7.24
12	.039	.014	.144	.175	.368	.133	4.146	1.577	5.971	1.914	17.06	11.23
$\bar{X}$	.016	.020	.217	.191	.978	.566	4.47	1.95	6.64	2.86	15.16	10.44
S.D.	.021	.029	.129	.148	.621	.393	1.81	1.41	2.10	2.48	2.58	5.77

Continued .../

Appendix XXVII (Continued)

Rhizome nodes (axillary buds) plant^{-1}

Individual	24 Jan.		11 Feb.		26 Feb.		27 March		17 April		19 June	
	R	S	R	S	R	S	R	S	R	S	R	S
1					125	115	373	395	569	256	762	353
2					56	101	407	248	561	333	1247	1424
3					51	112	364	68	608	526	1018	532
4					85	215	404	201	435	592	911	583
5					42	29	345	305	794	101	841	528
6					151	48	419	400	737	55	932	942
7					99	32	348	75	394	96	896	962
8					38	36	348	177	530	694	763	392
9					193	68	377	41	540	84	739	366
10					139	44	48	228	666	58	1046	607
11					124	23	220	38	529	681	1148	905
12					63	14	303	211	582	242	1006	96
$\bar{X}$					97	70	330	199	579	310	942	645
S.D.					49.6	57.7	103.5	127.0	113.4	250.2	158.2	358.5

Percentage of buds active

1					15.2	0	1.9	5.1	4.0	2.7	.5	2.3
2					5.4	1.0	3.4	2.8	3.7	.6	1.1	2.5
3					0	3.6	4.7	0	7.2	1.5	1.8	2.8
4					7.1	0	5.9	2.5	2.1	0	1.3	1.0
5					14.3	0	4.3	6.9	4.7	0	2.7	0
6					13.9	0	8.8	4.8	3.7	0	1.0	2.8
7					6.1	0	0	0	1.3	0	.2	0
8					2.6	16.7	5.2	2.8	7.4	3.6	1.7	17.6
9					6.2	0	0	0	5.4	0	.5	1.6
10					6.5	6.8	0	0	.6	0	2.8	.2
11					7.3	0	4.5	0	1.7	4.8	1.9	2.7
12					4.8	0	4.3	0	5.3	0	4.2	0
$\bar{X}$					7.5	2.3	3.6	2.1	3.9	1.0	1.6	2.8
S.D.					4.70	4.98	2.69	2.47	2.21	1.58	1.15	4.81

Appendix XXVIII Means of the dry weights and of the arcsine - transformed percentage data from the fragmentation and burial experiment (Exp. 2, Chapter 5).

a) percentage of planted fragments which remained partly or wholly undecayed and with at least one emerged shoot

	length of rhizome fragment (cm)			
depth of planting	4	8	16	
2.5	1.517	1.464	1.571	s.e. (mean) of six replicates was .0883
5.0	.985	.936	1.356	
10.0	.208	.393	.829	

b) number of shoots as a percentage of number of planted buds on fragments remaining undecayed

	4	8	16	
2.5	1.318	.866	.810	
5.0	1.097	.749	.766	.0576
10.0	.860	.674	.650	

c) percentage of active buds forming emerged shoots

	4	8	16	
2.5	1.571	1.424	1.539	
5.0	1.511	1.520	1.435	.1600
10.0	.628	.936	.926	

d) number of shoots as a percentage of the total number of buds planted

	4	8	16	
2.5	1.311	.846	.810	
5.0	.885	.564	.760	
10.0	.464	.401	.528	

e) total dry weight shoot^{-1} (g)

	4	8	16	
2.5	7.36	7.87	7.58	
5.0	8.50	6.91	7.16	.1365
10.0	.30	2.68	3.83	

f) rhizome dry weight shoot^{-1} (g)

	4	8	16	
2.5	.69	.71	.71	
5.0	.72	.63	.65	.1356
10.0	.02	.14	.43	

Note: In this and other appendices, the arcsine transformations were made as: $y = (\sin^{-1}\sqrt{\frac{x}{100}}) \,/\, 57.2958$ where y is the transformed value expressed in radians, and x is the original percentage value.

Appendix XXIX Seasonal bud activity data from experiment 3, Chapter 5. Values are the means of 4 observations.

Site 1			Site 2		
sampling date	% bud activity (arcsine)	dry weight shoot^{-1} (g)	sampling date	% bud activity (arcsine)	dry weight shoot^{-1} (g)
13/10/77	1.510	2.0	20/ 7/78	1.496	-
10/11	1.423	1.66	19/ 8	1.571	1.05
8/12	1.294	1.49	22/10	1.404	1.14
16/ 1/78	1.301	1.99	20/11	.888	.531
2/ 2	1.249	2.15	s.e. (mean)	.0576	.1050
8 /3	1.434	2.12	of 4 obs.		
17/ 4	1.444	2.10			
s.e. (mean)	.0545	.170			
of 4 obs.					

Appendix XXX Early development of plants from 10 cm - rhizome fragments planted at two times of the year (summer, autumn), (Experiment 4, Chapter 5). Values are means of 6, 5-plant replicates; shoot number as a % of the number of planted buds in parenthesis; weights in g dry matter 5 plants^{-1}.

summer-planted (14 Nov. 1978)

Harvest date	total shoot no.		emerged shoot no.		plant rhizome dry weight	new rhizome dry weight	vertical subter--ranean shoot dry weight	root dry weight	aerial shoot dry weight
26 Nov. 1978	11.8	(61)	0	(0)	.85	0	.06	0	0
2 Dec.	10.7	(55)	5.5	(28)	.74	0	.08	.007	.04
8 Dec.	11.0	(56)	7.8	(40)	.74	0	.10	.02	.17
14 Dec.	11.7	(60)	9.5	(49)	.71	0	.14	.03	.40
20 Dec.	9.7	(50)	8.9	(46)	.77	.007	.23	.11	.94
26 Dec.	9.8	(50)	9.7	(50)	.80	.127	.34	.24	2.12
1 Jan. 1979	11.2	(57)	11.0	(56)	1.13	.537	.72	.97	5.47

autumn-planted (17 April 1979)

30 Apr.	9.5	(46)	0	(0)	.92	0	.02	0	0
7 May	8.3	(40)	0	(0)	.72	0	.04	.001	0
21 May	9.5	(46)	4.5	(22)	.77	0	.08	.001	.01
29 May	8.3	(40)	6.5	(32)	.61	0	.07	0	.02
5 June	10.5	(51)	9.0	(44)	.68	0	.09	0	.04
18 June	8.8	(43)	7.7	(38)	.61	0	.09	0	.06
1 July	10.5	(51)	10.2	(50)	.77	0	.19	.007	.14
17 July	9.2	(45)	8.3	(40)	.79	.001	.21	.03	.22
30 July	9.2	(45)	9.2	(45)	.83	.002	.24	.06	.31
4 Sept.	8.3	(40)	8.3	(40)	1.00	.07	.39	.19	.78
30 Sept.	7.5	(37)	7.5	(37)	1.26	.45	.54	.45	2.08

Appendix XXXI The occurrence of new rhizomes on shoots with varying numbers of aerial leaves, over all harvests for both summer and autumn plantings (experiment 4, Chapter 5).

summer-planted (14 Nov. 1978)				autumn-planted (17 April 1979)			
leaf no. shoot^{-1}	no. of shoots	no. of shoots with new rhizomes	% of shoots with new rhizomes	leaf no. shoot^{-1}	no. of shoots	no. of shoots with new rhizomes	% of shoots with new rhizomes
1	0	0	-	1	12	0	0
2	10	0	0	2	39	0	0
3	58	1	1.7	3	82	0	0
4	64	1	1.6	4	79	0	0
5	36	2	5.6	5	66	0	0
6	35	15	42.9	6	48	2	4.2
7	35	25	71.4	7	47	27	57.5
8	21	16	76.2	8	25	20	80.0
9	20	18	90.0	9	17	17	100.0
10	16	15	93.8	10	6	6	100.0
11	7	7	100.0	11	2	2	100.0
12	2	2	100.0	12	2	2	100.0
13	2	2	100.0	13	1	1	100.0
14	2	2	100.0				
15	0	0	-				
16	0	0	-				
17	1	1	100.0				
18	1	1	100.0				

Appendix XXXII Depth distribution of rhizomes (including attached roots). Values are kg dry matter m^{-3} of soil; percentage of total in parenthesis.

	depth (cm)				
sample	0 - 2.5	2.5 - 5.0	5.0 - 7.5	7.5 - 10	Total
1	14.1 (58)	9.7 (40)	.544 (2)	.008 (.03)	24.4
2	10.8 (40)	14.0 (51)	2.1 (8)	.424 (.02)	27.3
3	16.2 (58)	10.6 (38)	1.1 (4)	.164 (.01)	28.1
4	16.1 (63)	7.7 (30)	1.6 (6)	0 (0)	25.4
5	6.7 (38)	8.8 (49)	2.3 (13)	.036 (.20)	17.8
mean	12.8	10.2	1.5	.126	
standard deviation	4.04	2.40	.72	.179	

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