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FIELD STUDIES OF LEAF GROWTH AND
DEVELOPMENT IN THE LEEK (Allium porrum L.)

Janette Ruth Brown, B.Sc. (Hons)

A Thesis Submitted to the University of Glasgow
for the Degree of Master of Science

Department of Plant Sciences,
West of Scotland College
Auchincruive, Nr Ayr
SCOTLAND

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SUMMARY

This research involved field studies of the leek (Allium porrum L.), which were based at the West of Scotland College, near Ayr. The leek provided a relatively simple plant system for leaf growth research, with vegetative growth and development of directly sown and transplanted crop stands being investigated (using both non-destructive and destructive methods of analysis).

A co-ordinated response to accumulated temperature of leaf initiation (plastochron $100^{\circ}\text{C days} > 0^{\circ}\text{C}$) and extension of the leaf blade and sheath resulted in the regular appearance of leaves. Each successive leaf required an additional 32°C days between initiation and tip appearance, resulting in a phyllochron of 132°C . This allowed for the progressive increase in 'sheath' height. With each successive leaf, the rate of leaf extension remained constant, but the duration of leaf expansion increased progressively, to produce progressively larger leaves. Overall, plants showed a relatively simple ontogenetic trend, in the absence of reproductive development. In contrast to other monocotyledonous crops, it was found that the rate of change of daylength at crop emergence was not an important environmental factor controlling leaf development. Seasonal variations in leaf development suggested that factors which vary between seasons may be involved in developmental control, with solar radiation being one possibility.

The effects of rust disease (Puccinia allii Rud.) were also studied in field-grown leeks. Infection of leek leaves was found to affect both components of crop growth rate (leaf area index, determining solar radiation interception, and photosynthetic efficiency). Although the production, and final dimensions, of leaves appeared to be unaffected by the presence of the rust fungus, the life span of leaves was reduced via accelerated senescence. However, the resultant depression of leaf area index did not occur until a relatively late stage in the life of the crop. The effect of rust disease on photosynthetic efficiency was found to be the more important factor causing reduced crop yield, with net assimilation being depressed by infection.

I INTRODUCTION

The leek (Allium porrum L.) provides an ideal plant system for studies of leaf growth and development. Due to the biennial nature of the crop, plants have a simple vegetative structure throughout the first growing season, with no flowers to act as sinks for photosynthetic assimilates. Leeks are large, unicum and usually produce at least twenty leaves before the onset of flowering in autumn. This apparently simple plant system would seem well suited to leaf growth research; but, relatively few studies have been made (eg. Bonnet, 1976b). By comparison, cereals have been extensively studied, despite the fact that they have a much shorter vegetative phase; that only about ten leaf primordia are initiated before spikelet primordia are formed; and, that leaf primordia accumulate on the apex, making it difficult to determine when rapid expansion of a leaf begins. Leeks provide better experimental material, particularly since accumulation of leaf primordia on the stem apex does not occur; once initiated, they continue to develop (Bonnet, 1976a). This allows meaningful estimates of the time from leaf initiation to appearance to be made.

In 1983 preliminary investigations were carried out at the West of Scotland College which established some basic information on leek growth and development (Walters & Hay, unpublished). Field experiments were designed to develop this preliminary work, and study quantitatively vegetative growth and development of the leek plant using both non-destructive and destructive methods of

analysis.

The main aims were:

- i) To study the co-ordination of events leading to leaf appearance;
- ii) To study the ontogenetic trends in leaf extension and in leaf dimensions;
- iii) To study the effects of infection by leek rust (Puccinia allii Rud.) on leaf growth and development.

II LITERATURE REVIEW

2.1 The Leek Crop

The leek (Allium porrum L.) is a biennial plant of the monocotyledonous family Liliaceae. It has been cultivated since prehistoric times (Brouk, 1975) and probably originated from the Levant in the eastern Mediterranean (Langer & Hill, 1982). The Romans are thought to be responsible for distributing leeks across Europe, and into England (Lovelock, 1972).

During the first year of growth, only vegetative plant organs are produced, and the plant is usually harvested at the end of this stage. This can be carried out at sixteen to twenty weeks from planting (Tindall, 1968). The harvested crop consists of enlarged leaf sheaths which are tightly wrapped around each other to form what is often referred to as a pseudostem. During the second year of growth the plants become reproductive, with flowers borne in a compound umbel (Langer & Hill, 1982).

In recent years the leek has increased in popularity as a winter vegetable (MAFF, 1982). This has led to considerable intensification of production, particularly of leeks destined for pre-pack outlets. Some 1700 hectares were grown in the United Kingdom by 1983 (Scopes & Ledieu, 1983). This figure had increased to 2414 hectares in 1985 (ESCA, personal communication). It is an

important economic crop plant, having one of the highest gross margins per hectare.

2.2 Vegetative Growth and Development of the Leek

2.2.1 **General**

The literature available on leeks gives an abundance of information on agronomic aspects; but, there is a paucity of information relating to growth and development.

Perhaps the most notable work was carried out in France by Bonnet in the 1970's. Bonnet reviewed botanical and agronomic aspects of the leek (1976a), producing a very detailed account of the morphological development of the plant. Both vegetative and reproductive phases of development were described, in a largely pictorial manner.

Bonnet followed this review with work on growth and development of the leaves of field grown leeks (1976b), comparing plants grown at two different planting depths. Part of his investigation included a quantitative study of the leaves.

2.2.2 **Germination and Development of the Seedling**

The leek exhibits hypogeal germination, characteristic of all Allium species (Jones & Mann, 1963; Bonnet, 1976a).

Germination begins when the primary root, or radicle, breaks out of the seed, followed by the cotyledon. The tip of the cotyledon remains inside the seed, where it absorbs the mobilised food reserve of the endosperm. As the radicle grows downwards, the cotyledon elongates to form a sharp bend, the knee or hook, which breaks the soil surface. At this stage the plant has emerged.

After the hook has reached a height of 5-7.5 cm, elongation of the section between hook and seed ceases, while the segment between hook and stem continues to elongate, thus pulling the tip of the cotyledon free from the soil.

The cotyledon slowly straightens out by unbending at the knee, lifting the seed coats and endosperm upward. It has a simple, tubular structure, with the base enclosing the shoot apex. There is a small basal opening in the cotyledon, through which the first true leaf finally emerges. The seedling is then established.

2.2.3 The Development of Stem and Leaves

Once the seedling is established, the young leek plant continues to produce new leaves. At the same time as the appearance of leaves, the main root (developed from the radicle) withers and is replaced by adventitious roots (Bonnet, 1976a).

The stem takes the simple form of a flattened cone (Bonnet, 1976a), with very short internodes. It remains like this, beneath the soil surface, throughout the vegetative phase, resulting in the formation of a rosette.

Leaves are the only aerial organs formed by the leek during the vegetative phase, and make up the largest part of the plant (Dragland, 1972). As Bonnet (1976b) points out, the plant is made up almost entirely of leaves, with stem reduced to a "platform" and roots only representing 5 to 8 per cent of the total dry weight.

The leaves have a distinctive alternate phyllotaxis, where the angle between successive primordia is 180° , so leaves develop in two ranks. They fit inside each other at their white sheathed bases, forming a firm structure which is commonly known as a false stem, or pseudostem, to distinguish it from the true stem which lies beneath the soil surface.

Each glaucous green leaf blade, or lamina, is held erect when it first appears. However, as it increases in size it bends over to assume a more prostrate type of growth habit.

Bonnet (1976b) made a study of leaf production and leaf growth of leeks cultivated in the field, using two cultivars and two different planting depths. He observed

that, "foliar growth is of the allometric type: the sheath begins to elongate one month later than the blade; as the sheathing base is formed as early as the primordium stage hence its growth is inhibited during more than two months". It was also noted that each successive leaf formed had a final length greater than the last. This was reflected in increasing lengths of both blade and sheath. For example, with the variety Bleu de Solaise, transplanted at a depth of 80 mm, leaves numbered 6 and 7 had final lengths of 500 mm and 620 mm, lamina lengths of 400 mm and 510 mm and sheath lengths of 100 mm and 110 mm respectively.

While new leaves form throughout the vegetative phase, older leaves begin to senesce, starting at their extreme tips, and eventually withering completely. This posed a problem in Bonnet's studies, for by the time young leeks were transplanted to the field, some leaves had already withered. After eliminating external withered leaves, plants were then marked, or tagged, with the outermost leaf taken as "Number 1". Thus, leaves of the same relative numerical order were not necessarily of the same actual status.

2.3 Leek Production Systems

Two main production systems are used in leek cultivation (eg. MAFF, 1982). They can be grown by drilling seeds

in the field, or by sowing in seedbeds and transplanting. Advantages of the latter include greater flexibility and intensity of crop rotations, and the leeks are likely to have a greater length of blanched stem. Kolata (1971) found that, in four year trials, transplanted leeks generally overwintered better and gave more uniform and heavier plants in the spring than direct sown leeks.

Plant growth rate is related to the efficiency with which increasing radiation is intercepted and converted into useful plant products (Biggs & Fordham, 1985; Hay & Walker, 1989). Direct-seeded crops often grow slowly through the seedling stages, showing poor light interception as much of the radiation falls on bare soil. Light interception will improve directly with leaf canopy cover. For some commercial crops, a leaf area index of at least 3 is necessary to allow for 90-95 per cent interception of incoming radiation (eg. potatoes and wheat). Transplanted vegetables produce leaf canopy much faster than seeded crops and can retain this advantage.

However, because transplanting involves a considerable amount of labour, it may not be very cost-effective as a cultural procedure. Also, there can sometimes be problems with transplanting checks on growth (Biggs & Fordham, 1985). Thus, drilling of the crop in situ is increasing in popularity.

Milanov (1972) compared growing leeks by transplanting and drilling (without thinning). For both methods, the earlier the sowing, or planting, date the higher the yield and larger the plants. Despite the fact that transplanted leeks were larger, the drilling method resulted in higher total yield and was considerably cheaper.

2.4 Factors Affecting Plant Growth and Development

2.4.1 **Temperature**

The effects of temperature on plants are many and varied (eg. Sutcliffe, 1977). However, for a plant such as the leek, harvested in the vegetative state, the most important effects of temperature are on seed germination and leaf development, including expansion as well as appearance.

2.4.1.1 **Germination**

There is a minimum and maximum temperature for the seeds of each species, and outside this range germination will not occur.

Bonnet (1976a) suggests that the optimum range for leek germination is between 13°C and 23°C. Biggs and Fordham (1985) suggest the range of 7°C to 21°C, over which leeks will germinate well. Whatever the correct minimum and maximum, the leek is considered to have a narrow range

for germination, compared to other monocotyledonous crops. For example, barley, wheat and rye grains will not germinate below 3-5°C or above 30-40°C, while maize grains have a germination range between about 8°C and 44°C (Sutcliffe, 1977).

2.4.1.2 Leaf Development

As far as leeks are concerned, only the recent work of Hay and Brown (1988) has involved any detailed research into the effects of temperature on leaf development.

Prior to this work, the literature on leeks shows very scant and often generalised information on temperature and vegetative growth, largely confined to assessing total yield or dry matter accumulated at the end of an experimental period.

Dragland (1972) found that fresh and dry weights of leeks increased with rising temperature (up to 21°C) and increasing daylength. Salter, Akehurst and Morris (1985) showed that, with a series of planting dates, later plantings resulted in progressively lower yields. Comparisons with meteorological data showed that decreasing yields were associated with decreasing values of accumulated solar radiation and accumulated day-degrees during field growth.

Although the temperature relations of leaf development in leeks may not have received much attention prior to Hay and Brown (1988), other crop plants have been extensively studied, particularly the cereals (eg. Gallagher, 1979; Baker, Gallagher & Monteith, 1980; Baker and Gallagher, 1983; Kirby, Appleyard and Fellowes, 1982, 1985). Much of this work has been reviewed by Ong and Baker (1985), with the concept of accumulated temperature assessed, several important responses of leaf growth to temperature discussed and the difficulties of examining leaf growth in the field highlighted.

Accumulated temperature, or thermal time, can be defined as the time perceived by the plant as a function of temperature (Monteith, 1977b; Ong & Baker, 1985). It is generally used to analyse the rate of plant development, including leaf growth, because it offers a way of dealing with day-to-day variation in temperature. However, there are uncertainties over the choice of base temperature (T_b) in various studies (Hay & Delécolle, 1989). This is largely due to the fact that T_b is obtained by extrapolation, usually over several degrees, and the accuracy of this can be influenced by sensitivity of leaf growth to such factors as humidity, photoperiod and water deficit. However, in general, T_b varies from 0-3°C for temperate crops.

The production of leaf primordia, leaf appearance, laminar expansion and the duration of leaf growth of field grown wheat and barley can all be described in terms of accumulated temperature (Gallagher, 1979; Baker and Gallagher, 1983). Leaf primordial number and appearance stage increased linearly with accumulated temperature, whereas only 90 per cent of laminar and leaf length growth and 80 per cent of laminar width growth did so. When expressed in accumulated temperature, wheat leaves had a similar duration of linear growth (210°Cd ; s.d. 30°Cd), and the first seven leaves of barley had a shorter duration of linear growth (151°Cd ; s.d. 8°Cd) (Gallagher, 1979).

Baker et al. (1980) and Kirby et al. (1982) found that leaf appearance rate in the field was also affected by the rate of change of daylength at plant emergence. Baker et al. (1980) plotted the mean rate of leaf appearance in thermal time (R') against the rate of daylength change at crop emergence ($d\phi/dt$), for winter wheat with a range of sowing dates from early October to early March. The equation of the fitted line ($P < 0.001$) was: $y = a + b(d\phi/dt)$. When R' has units of $(^{\circ}\text{C day})^{-1}$ and $d\phi/dt$ is in h day^{-1} , $a = (10.6 \pm 0.2) \times 10^{-3} (^{\circ}\text{C day})^{-1}$ and $b = (0.04 \pm 0.004)(^{\circ}\text{C day})^{-1}$. The rate of leaf emergence per $^{\circ}\text{C day}$ became faster the later the sowings, until April when the effect was reversed. Kirby et al. (1982) found a similar response in barley, when rates of leaf emergence

were examined with respect to rate of change of daylength. The fitted line was given by the regression: $y = 0.0129 + 0.0430 (d\phi/dt)$; $r = 0.925$; $P < 0.01$. However, a similar response in controlled environments could not be detected.

It is widely accepted that the total amount of dry matter accumulated by a crop is closely related to the amount of radiation which is intercepted by the foliage during growth (eg. Monteith, 1977a; Elston, 1980). Thus, any constraint on the seasonal distribution of leaf area may have an effect on crop yield. It is clear that for cereals, at least, leaf growth is strongly dependent upon environmental temperature, which therefore could represent an important constraint, through any adverse effects on leaf growth.

2.4.2. The Effects of Obligately Biotrophic Fungal Pathogens on Crop Growth and Yield.

2.4.2.1 **General**

Rust and powdery mildew fungi are obligate biotrophs, which depend upon the presence of viable host tissue to complete their development (Walters, 1985). Thus, they do not kill the host plant outright, but have a deleterious effect upon it. A number of cellular processes and constituents necessary for host plant growth and development are affected during infection (Hutcheson &

Buchanan, 1983). However, disease-susceptible plants grow and yield less than resistant plants, largely because pathogens interfere with photoassimilation of CO₂ (Ayres, 1982). Pathogens also utilise compounds obtained from the host for their own growth and development.

Walters (1985) reviewed the physiological and biochemical responses of the host plant to infection by obligately biotrophic fungal pathogens, basing much of his discussion on the rust and powdery mildew fungi. Clearly, there are wide-ranging effects on the host plant, including disruption of CO₂ exchange. Infection usually leads to a reduction in the rate of net photosynthesis (eg. Livne, 1964) and a stimulation of dark respiration. In some systems there is also a reduction in photorespiration (Walters, 1985). An increase in dark respiratory results in newly-fixed assimilate being lost via respiration processes (Walters, 1985). The plant uses photoassimilates to synthesise materials such as phytoalexins, which are used in defence mechanisms, and polysaccharides (eg. callose) which are used to strengthen or repair cell walls at points of fungal attack (Ayres, 1982). Thus, photosynthate is lost which would otherwise be used for plant growth. The pathogen also uses photoassimilates to support fungal growth and respiration. A rust fungus, producing 100,000 spores per day can take 10-15 per cent of the daily photoassimilate produced by the colonised area, which is also

photosynthesising at a reduced rate (Ayres, 1982).

Reduced photosynthetic activity coupled with loss of assimilates to respiration and to the pathogen, result in less dry matter being invested in new leaves, so that the photosynthetic capacity of the plant is reduced. Lowered yields may be directly attributed to a reduction in photosynthetically active leaf area (Walters & Ayres, 1981).

Uninfected leaves of an infected plant may show a stimulation of photosynthesis. This could allow the plant to compensate for the loss of assimilates to the fungus, and, thus, the yield of lightly-infected plants may be protected to some extent. Indeed, such compensation may be critical to the survival of heavily-infected plants (Walters, 1985).

On a whole plant basis, infection of barley by powdery mildew resulted in decreased leaf area, which paralleled decreases in the dry weight of tops. Also, net assimilation rates decreased as a result of infection (Last, 1962).

Yellow rust was found to have a considerable effect on yield of a spring wheat (Doodson, Manners & Myers, 1964). In severely-infected plants, yield was reduced by as much as 65 per cent. There was a marked effect on

general growth and vigour of plants, with leaf growth being retarded, such that final length and breadth of individual leaves were greatly reduced.

Owera, Farrar and Whitbread (1981) showed that green leaf area was reduced by brown rust infection of barley. They recognised this as a major effect of disease, along with increased respiration of the leaf-rust system.

Lim and Gaunt (1986) studied epidemic development, green leaf area and yield in spring barley, infected with powdery mildew and leaf rust. In contrast to Last (1962), Doodson et al. (1964) and Owera et al. (1981), where plants were grown in controlled environments, Lim and Gaunt (1986) studied field-grown plants. Both diseases caused large yield losses, particularly when early infection occurred. Early epidemics of powdery mildew affected plant growth directly because of lesions and associated chlorosis. They also had an indirect effect at later growth stages, when the disease was no longer present, by reducing leaf size, thereby reducing green leaf area. This contrasts with work by Jenkyn (1976) and Carver and Griffiths (1981, 1982) who attributed reduced green leaf area to increased disease and senescence, in barley plants infected with powdery mildew.

Furthermore, reductions in yield associated with early infection were not compensated for during later crop growth (when disease was no longer present). Late epidemics of rust had no effect on leaf size, therefore timing of infection was important. Lim and Gaunt (1986) concluded that green leaf area was a better measure of disease than percentage disease severity in yield loss studies.

2.4.2.2 Leek Rust

Leek rust (Puccinia allii Rud.) is common on leeks in the Midlands and South Wales (Western, 1971), and is becoming more common in other leek-growing areas. The disease can be a problem after a succession of mild winters because such weather prevents any slowing down in development and production of rust pustules and rust spores. General intensification in leek production can lead to successional cropping on some farms (Scopes and Ledieu, 1983). Growers try to produce leeks earlier in the year so that crops overlap in time. Because live leek tissue can then be present throughout the year, the rust life cycle is effectively unbroken. Outer leaves of infected plants bear bright orange circular to elongate pustules (uredosori) between the leaf veins. An additional symptom can be chlorotic spotting of the leaf (Dixon, 1981). The crop is disfigured rather than destroyed.

Many leeks are now pre-packaged for sale under transparent covers. This type of packaging calls for very high quality standards, with blemish-free leeks being demanded. In this respect, a disease such as leek rust can cause considerable financial loss to the grower. Older, infected leaves must be removed before a plant can be sold. To achieve this, several outer leaves may have to be discarded, which decreases the weight of plant for sale.

In addition to these effects on the quality of leeks, rust disease can also affect crop yield. It is thought to reduce growth and delay maturation of plants for several weeks (Doherty, 1981).

A number of recent studies on the physiological and biochemical effects of leek rust on host plants have been carried out (Roberts & Walters, 1986, 1988a, 1988b, 1989). At a maximum of 30 per cent infection intensity, host plants showed a very large reduction in photosynthesis in infected leaves. This contrasts with a very large increase in photosynthesis in uninfected leaves, the result being that net photosynthesis per whole plant was slightly increased. However, growth of plants was reduced by about 30 per cent, so it was assumed that assimilates were probably translocated to infected leaves where dark respiration was greater by about 18-fold. Roberts and Walters (1989) showed that uptake and concentrations of

many nutrients (P, K, Ca, N) is increased in rusted plants, and therefore nutrients are not limiting growth under these circumstances.

The combination of adverse effects on both yield and quality means that the economic impact of leek rust can be quite considerable, and a cause for concern in badly-affected growing areas.

III MATERIALS AND METHODS

3.1 Experimental Site

Experiments were conducted at the West of Scotland College (Auchincruive Estate), latitude 55°29'N, longitude 4°33'W, altitude 30-46 m, situated 4.5 km ENE of Ayr. The area experiences a mild, maritime climate with an average annual precipitation of 1000 mm, with May and June being the driest months.

Weather was recorded at the Auchincruive Agrometeorological Station which is less than 0.5 km from experimental areas. Weekly summary charts were obtained for the course of the field experiments in order to assess the weather throughout the growing season. Meteorological conditions over the experimental period are presented in Figure 1, and compared with the 21-year mean (1965-85). Rainfall was well above average during July, August and September, accounting for 52% of the years rain (Walker & Kirkwood, 1986). This high rainfall was associated with fewer hours of bright sunshine.

The experimental sites have a sandy loam soil and have been in continuous use for annual crop research, over a number of years.

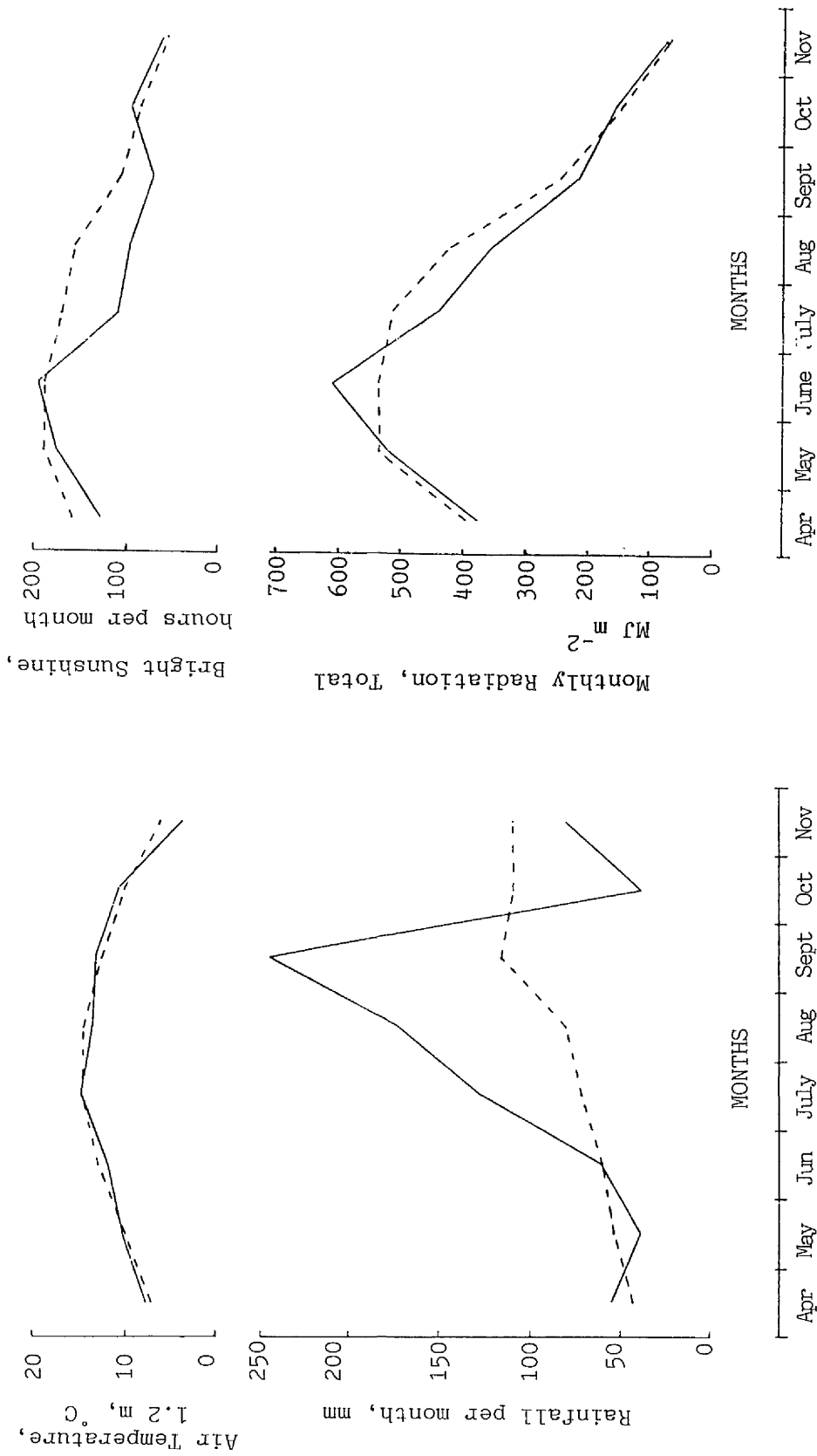


FIG. 1 Comparison of meteorological data for the year 1985 (solid line) which those of the 21-year average 1965-1985 (broken line), at Auchincruive Estate (Note that for radiation totals, the broken line represents only a 10-year average 1976-1985).

3.2 Experimental Design and Layout

The design and layout of the three main experiments carried out are summarised in Figure 2.

3.2.1 **Experiment 1**

This experiment involved primordia and leaf extension studies of leek plants. A large plot (12.0 x 6.0 m²) was direct drilled by hand on 3rd May. This was located at Templefield on the Auchincruive Estate.

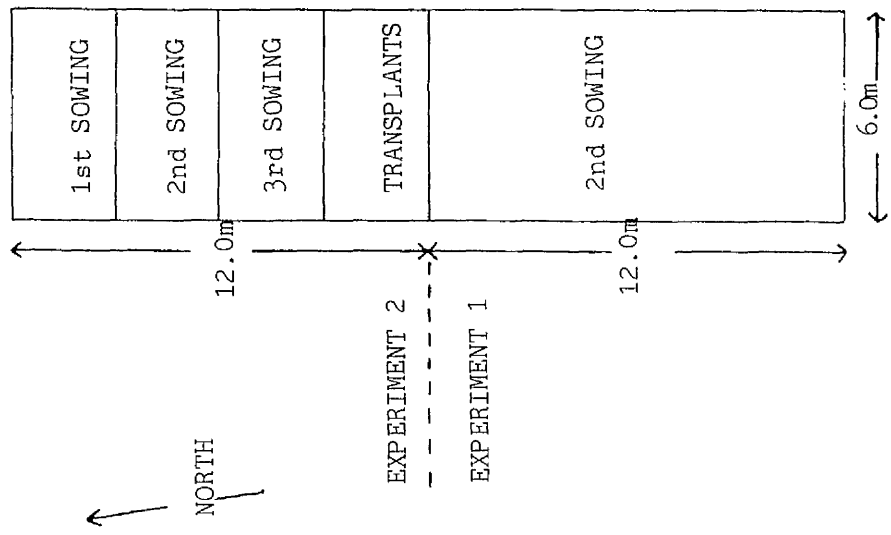
3.2.2 **Experiment 2**

This experiment involved plants of different sowing dates and methods of cultivation. The plot used was also 12.0 x 6.0 m², divided into four subplots (each 3.0 x 6.0 m²). Three subplots were direct drilled, with three different sowing dates employed - 19th April, 3rd May and 17th May. The remaining subplot was used for transplants, planted out on 12th June. The Templefield location was used for this experiment.

3.2.3 **Experiment 3**

This experiment was designed to examine healthy (H) and rust-infected (R) plants from the same growing area. A 10.0 x 5.0 m² plot of land was direct drilled on 18th May. Later, it was divided into healthy (fungicide sprayed) and rust-infected subplots using a 2 x 2 Latin Square arrangement. This simple experimental design was used because of the high probability of cross-infection

(a) TEMPLEFIELD



(b) DIAMONDFIELD

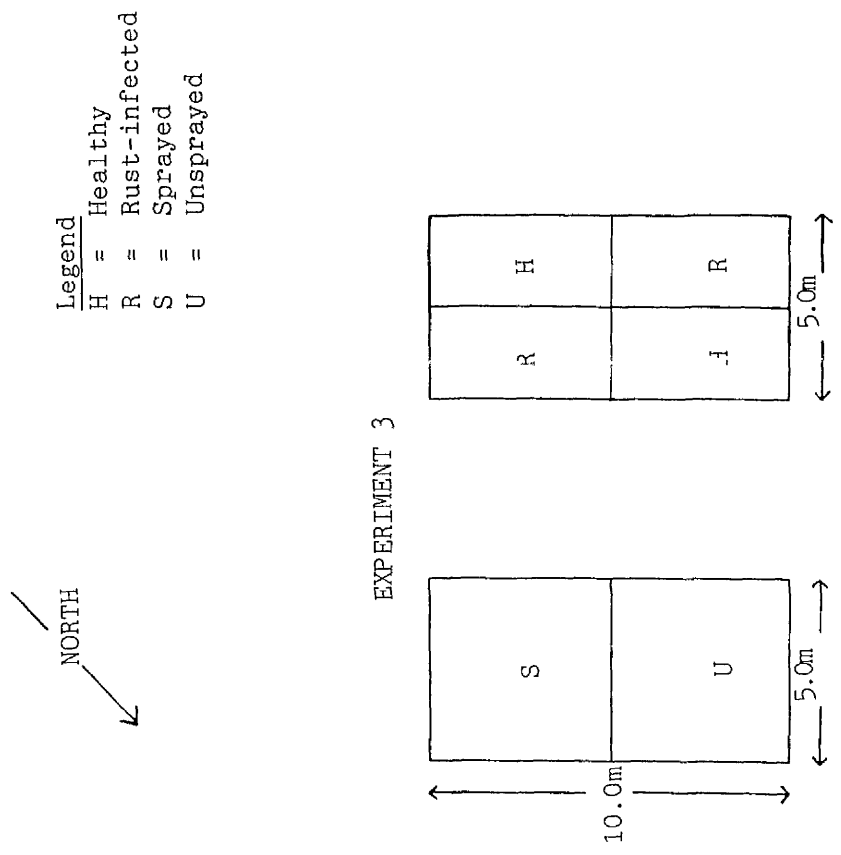


FIG. 2 Diagrams showing experimental design and layout. Experiments 1 and 2 are presented in (a). Experiment 3 is presented in (b).

(illustrated by the fact that even fungicide treated subplots eventually became infected).

An additional plot (10.0 x 5.0 m²) was also drilled on 18th May. It was divided into two subplots (each 5.0 x 5.0 m²), one sprayed with fungicide (S) and the other unsprayed (U). Assessments of plants from these subplots showed whether the fungicide used had any effects on plant growth and development.

The Diamond field location was used for this experiment.

3.3 Crop Establishment

Prior to this study, experimental areas were prepared (March-April) by rotavation, weed clearance and liming (to a pH of 6.5).

Leeks (cv. Autumn Mammoth - Goliath Selection) were grown from seeds supplied by Browns of Poulton, Seed Growers and Merchants. This variety is recognised as a traditional product in the leek market, and can be harvested from October through to February in all except the most severe winters (MAFF, 1982).

Two methods of leek cultivation were used - transplanting and direct drilling (by hand).

3.3.1. Transplanting

Seedlings for transplanting were sown in a glasshouse on 4th March in 17 cm pots of Fisons Levington Universal Compost. The glasshouse was ventilated, with a 24°C day/9°C night temperature regime. Natural daylight was extended to a 16-hour photoperiod (extension at low irradiance using HLRG high pressure Hg lamps).

When the third leaf had emerged, seedlings were transferred to trays and grown on in the glasshouse. Prior to transplanting, plants were "hardened off" in an outdoor cold-frame for a three week period.

On 12th June, plants with six true leaves were transplanted to the field in a 300 x 150 mm arrangement, giving a plant population density of 25 plants m⁻².

3.3.2 Direct Drilling

Seeds were sown by hand in drills 300 mm apart, seeds being evenly distributed along the drill length. Leek seeds are small, with small reserves, so the sowing depth was at the recommended 1-2 cm.

After emergence, plants were thinned to give 25 plants m⁻² (300 x 150 mm arrangement).

3.4 Experimental Management

All experimental plots were managed with weed control, fertiliser application and irrigation. Only Experiment 3 called for additional management procedures - fungicide application and rust inoculation.

3.4.1. **Weed Control**

A pre-emergence herbicide (Ramrod + Dacthal) was used on drilled plots, one week after sowing plants. Further weed control was carried out by hand (picking or hoeing) since regular use of herbicides can affect plant growth.

3.4.2. **Fertiliser Application**

Drilled plots received 200 kg Nha^{-1} , 44 kg $\text{P}_2\text{O}_5\text{ha}^{-1}$ and 83 kg $\text{K}_2\text{Oha}^{-1}$. This was applied in two equal applications at the recommended times of three and six weeks after emergence. Plots were not fertilised prior to sowing since high nitrogen levels can inhibit seed germination. With transplanted leeks, fertiliser was applied at the time of transplanting.

3.4.3. **Irrigation**

Plants were watered by hand immediately after sowing, to ensure rapid, even seedling establishment. Transplants were also watered immediately after transplanting. Thereafter, irrigation was carried out during any periods of dry weather.

3.4.4. Fungicide Application

In Experiment 3, it was necessary to spray "healthy" (H) plants with a fungicide, to protect them from rust infection in adjacent rust-infected (R) plots. Sprayed (S) plants were also treated with fungicide. The systemic fungicide Bayleton (Bayer) was chosen because it contains 25% w/w triademefon, the active ingredient which is recommended to give good control of leek rust (MAFF, 1982).

Bayleton was used at a rate equivalent to 2 kg a.i.ha⁻¹ in 200 l water, including wetting agent. It was applied at the time of rust inoculation of R plots (30th July), and thereafter at three-weekly intervals.

3.4.5. Rust Inoculation

The most satisfactory method of infecting plants with rust disease is by using a suspension of urediniospores in distilled water. This is painted on to the leaves of plants.

Rust stock was available from leek plants grown in isolation at the Botany Department glasshouse. Freshly-isolated spores from these infected stock plants were used in the following procedure.

Spores were removed from heavily-infected leaves using a moist camel hair brush. These were transferred to

approximately 50 ml distilled water. The brush was dipped into this water and the whole procedure repeated a number of times. When the spore suspension had reached a dark orange colour, it was suitable for use in inoculation.

Plants were inoculated once the fifth leaf was emerging. This is considered a suitable age for, if any younger, plants could be killed by the fungus, or, if older, problems could arise with adult plant resistance.

The ideal weather for inoculation is recommended as dry and slightly cloudy conditions, and the best time of day is around mid-afternoon, when humidity is reasonably high. Thus, it was necessary to spread inoculation over a few days (29th July to 2nd August) due to the number of plants involved.

Plants were inoculated by painting spore suspension liquid over every visible surface. Once plants were painted there was an incubation period of 10-12 days, after which signs of infection could be seen.

3.5 Measurements

3.5.1. **Experiment 1**

In experiment 1, plants were used for destructive

assessment of leaf development. Ten randomly-selected, but representative, plants were harvested at weekly intervals from 5th July (third true leaf stage) to 27th November. These were dissected to count and measure leaf primordia and young leaves extending inside the "pseudostem".

3.5.1.1. Plant Dissection

A binocular stereoscopic microscope, or 'dissecting' microscope, was used during dissection. This microscope was fitted with a zoom lens system, giving a range of magnifications from x1 to x4.

The dissection technique used followed that suggested by Kirby and Appleyard (1984) for cereals. They recommended that a minimum of five plants be examined at each harvest, to obtain a reliable estimate of apex development. Because leeks are known to be more variable than cereals, this number was doubled, and ten leek plants used at each harvest date.

Outermost, fully extended leaf structures were removed first, and length measured (leaf lamina + leaf sheath). Any senescent outer leaves were not measured.

Extending leaves were then removed (oldest to youngest) using a sharp mounted needle, and measured with a calliper rule.

Once the youngest exposed leaf was approximately 30 mm long, the plant was transferred to the dissecting microscope. The plant base was held in plasticine and fixed to the microscope stage for further dissection. With quick, precise work, the shoot apex could be exposed and primordia examined before losing too much water and shrivelling.

3.5.1.2. Dissection Measurements

Measurements were recorded under the headings:-

- i) Number of leaves inside sheath
- ii) Leaf lengths inside sheath (cm)
- iii) Longest sheath height (cm) above soil level
- iv) Overall plant height (cm)
- v) Number of leaf primordia
- vi) Total number of leaves + leaf primordia

In addition, the lengths of extended leaves were recorded (lamina + sheath).

Thus, information was collected on the number of appeared leaves; the number of leaf primordia on the apex; the total number of leaf structures initiated; and, the "pseudostem" length. Also, the measurement of length of fully extended leaves and leaves inside the pseudostem provided leaf extension data.

For this study the pseudostem was measured as the distance from the soil surface to the ligule of the youngest fully-expanded leaf. This is the distance above the soil surface which the tip of an expanding leaf must travel before it is visible (Hay & Brown, 1988). In the early stages of development of the leek plant, this is a relatively straightforward process. However, later in development, a number of leaves can be extending simultaneously causing crowding of tissues near the ligule of the youngest fully-expanded leaf. Thus, the leaf tip has to travel slightly further in order to appear. For this reason, the pseudostem lengths recorded became less accurate later in the growing season.

3.5.2. Experiment 2

Plants in all subplots (3 drilled + 1 transplanted) were used for two types of analysis - non-destructive and destructive analysis of growth and development.

3.5.2.1. Non-Destructive Analysis

For this type of analysis, plants were measured in situ. Twelve randomly-selected and uniform plants from each subplot were marked, or tagged, using loops of coloured wire.

At regular intervals throughout the growing season (approximately weekly), these plants were measured to obtain the following data:-

- i) Leaf length (cm)
- ii) Leaf breadth (cm) - at the widest point
- iii) Sheath height above soil level (cm)
- iv) Overall plant height (cm)
- v) Overall plant height (soil to tip longest leaf) (cm)

Appearing leaves were measured from the pseudostem, ie. from the youngest visible leaf ligule. When leaves were senescent, only the green leaf length was measured.

Thus, information was collected on the number of appeared leaves (leaf tip visible), plant height, and the dimensions of fully-expanded leaves (lamina length and width, sheath length).

3.5.2.2. Destructive Analysis

This involved harvesting ten plants from each subplot at regular intervals throughout the growing season. Each plant was dissected to separate leaf from pseudostem material. Older leaves were cut at the ligule until the last visible ligule (the youngest) was reached. The plant was then cut straight across at the ligule, giving pseudostem material and tops of emerging leaves.

Plant leaf area was measured using a Delta-T leaf area meter. At this stage, leaves were inspected for any signs of rust disease which, if present, was recorded.

Leaf and stem material for each plant was weighed to give fresh weight, then placed in a drying oven at 75°C. After 24 hours, or more, the samples could be reweighed to ascertain dry weights.

The following details were recorded:-

- i) Plant leaf area (cm^2)
- ii) Leaf blade weight (g) - fresh and dry weights
- iii) "Pseudostem" and sheath weight (g) - fresh and dry weights
- iv) Overall plant height (cm)
- v) Overall plant height (soil to tip longest leaf) (cm)
- vi) % leaf area infected - for rusted plants only

Thus, information was collected to allow a growth analysis of each stand using the curve-fitting procedure of Hunt and Parsons (1974). Their general-purpose computer program fits smooth curves to experimental data, then derives fitted values for growth-functions which may be plotted continuously. Functions of the type $1/Y \cdot dY/dX$, Z/Y and $1/Z \cdot dY/dX$ are used, where Y is whole-plant dry weight, Z is total leaf area and X is time. These functions yield, respectively, relative growth rate (RGR), leaf area ratio (LAR) and net assimilation rate (E). Cubic regressions are fitted to a time series of logarithmically transformed values of Y and Z, and standard errors are also calculated.

The Hunt and Parsons program is most suitable where data from a long series of 'continuous harvests' are available, as in this study. RGR, LAR and E were therefore assessed throughout the growing season.

Finally, disease development in any stand was closely monitored.

3.5.3 Experiment 3

Plants in all subplots (H, R, S and U) were used for non-destructive and destructive analysis of growth and development (see 3.5.2.1 and 3.5.2.2).

3.6 Additional Experiments

Following the field based experiments of 1985, additional glasshouse-based experiments were carried out in 1986. These provided a photographic record of stem apex development in the leek and information on the leaf extension zone in leek leaves.

3.6.1 Photographic Recording of Stem Apex Development

Glasshouse grown leeks were dissected to photograph the apex, and young extending leaves. An Olympus stereo microscope was used, fitted with a zoom lens system (x1 to x 4). The microscope was also fitted with Olympus PM-6 (compact) photomicrographic equipment and an Olympus photomicrographic exposure meter (Model EMM-

VI). A cold light source (Flexilux 150 HL Universal) was used to minimise drying and shrivelling of plant material.

3.6.2. Leaf Extension Zone Measurement

The needle method of Davidson and Milthorpe (1966) and Kemp (1980) was used to assess the length of leaf extension zone in successive expanding leaves.

Glasshouse grown leek plants, with 10 or 11 appeared leaves, were pierced transversely with a needle at 1 cm intervals from the position of the apex. Thus all leaves were marked at 1 cm intervals, and dissection of plants after 48 hours showed where the extension zone on various leaves was located, ie. where intervals exceeded 1 cm.

IV RESULTS

4.1 Growth and Development in the Leek

4.1.1 **Vegetative Development**

Development of the young leek plant is shown diagrammatically in Figures 3 and 4. Figure 3 shows various stages seen during the course of the field experiments. These are described in detail in Section 2.2.2. Figure 4 shows development of stem, leaves and roots of a young leek plant, which is described in Section 2.2.3.

4.1.2. **Development of Leaves at the Leek Stem Apex**

The development of leaves at the leek stem apex was recorded photographically (Plates 1, 2, 3, 4). Leaves appear to develop in much the same fashion as those of cereals and grasses (Langer, 1979). Early in the development of the leaf, lateral expansion of the primordium results in the apex being fully encircled by the base of the leaf. At the same time, elongation occurs so that the leaf forms a hood over the apex.

In this way, young leaves are produced throughout the vegetative phase of the leek. However, at the onset of flowering, further leaf initiation ceases and the apex undergoes dramatic morphological changes, with a complex arrangement of floral initials produced.

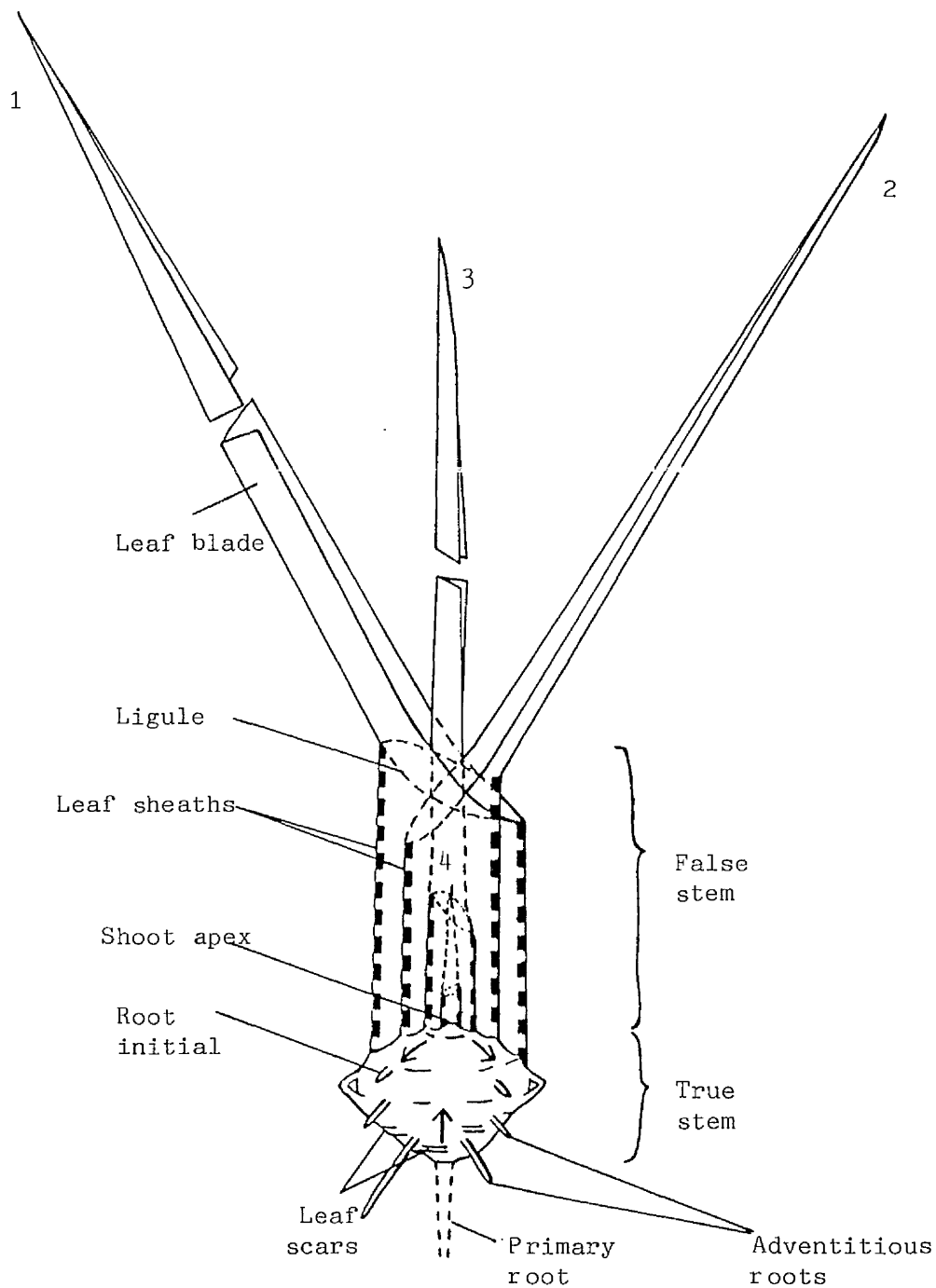


FIG. 4

A schematic diagram of the development of the stem, leaves, and roots, in a young leek plant. Each new leaf arises at the stem or shoot apex, leaf 1 being the oldest and leaf 4 the youngest of the four leaves shown. As the stem grows upwards, it also broadens, as shown by the divergent arrows in the diagram. New roots continually arise in the younger (upper) part of the stem. The space between adjacent leaf-sheaths is much exaggerated. (Adapted from Jones & Mann, 1963; Bonnet, 1976b).

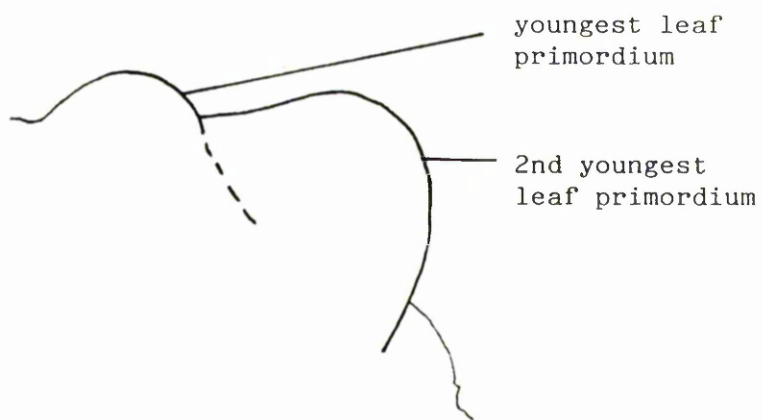
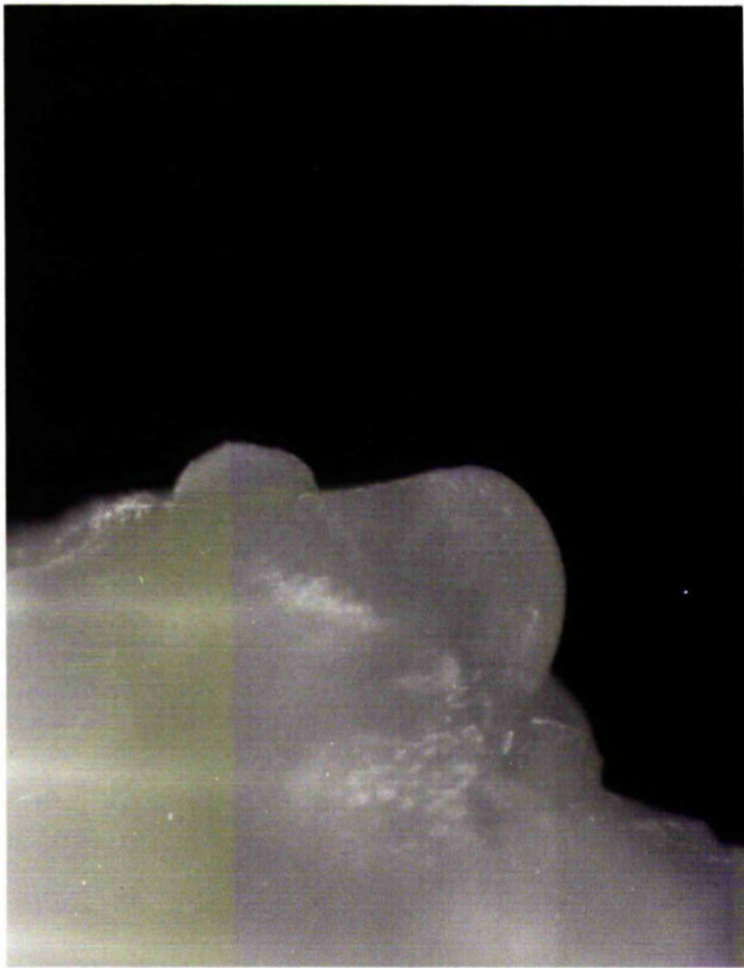


PLATE 1 Dissection photograph showing two leek leaf primordia on the stem apex, seen under a stereo microscope (x 10 eyepiece, x3 zoom lens).

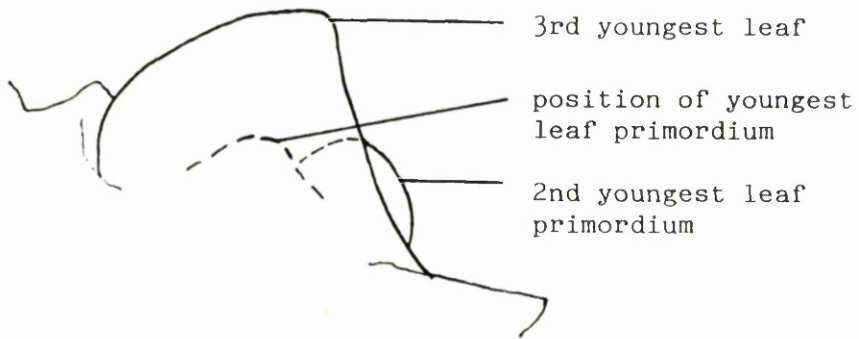
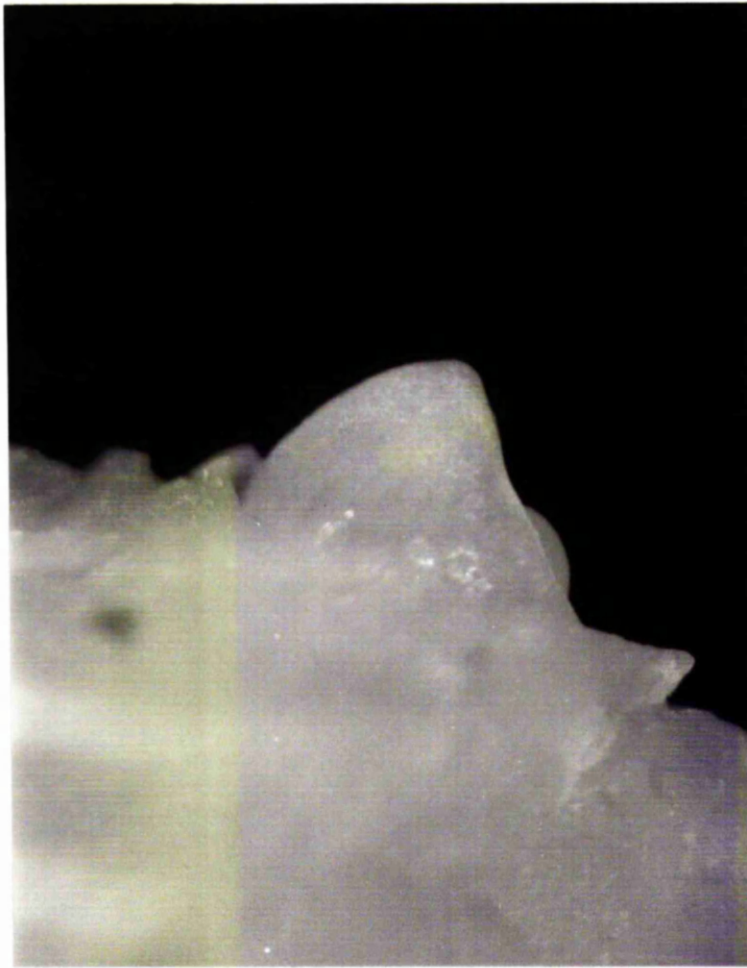


PLATE 2

Dissection photograph showing the third youngest leek leaf developing inside the 'sheath', seen under a stereo microscope (x10 eyepiece, x1.7 zoom lens).

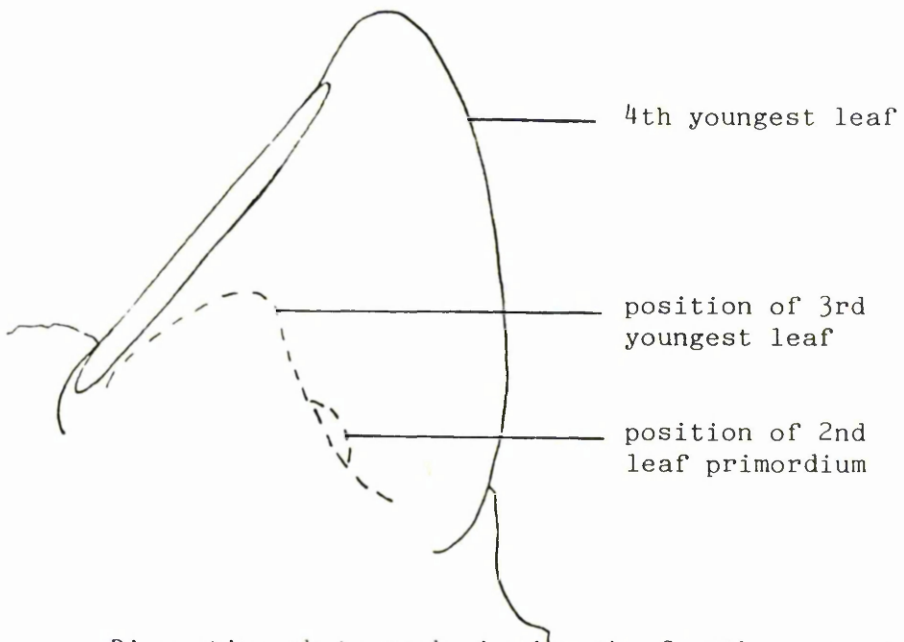
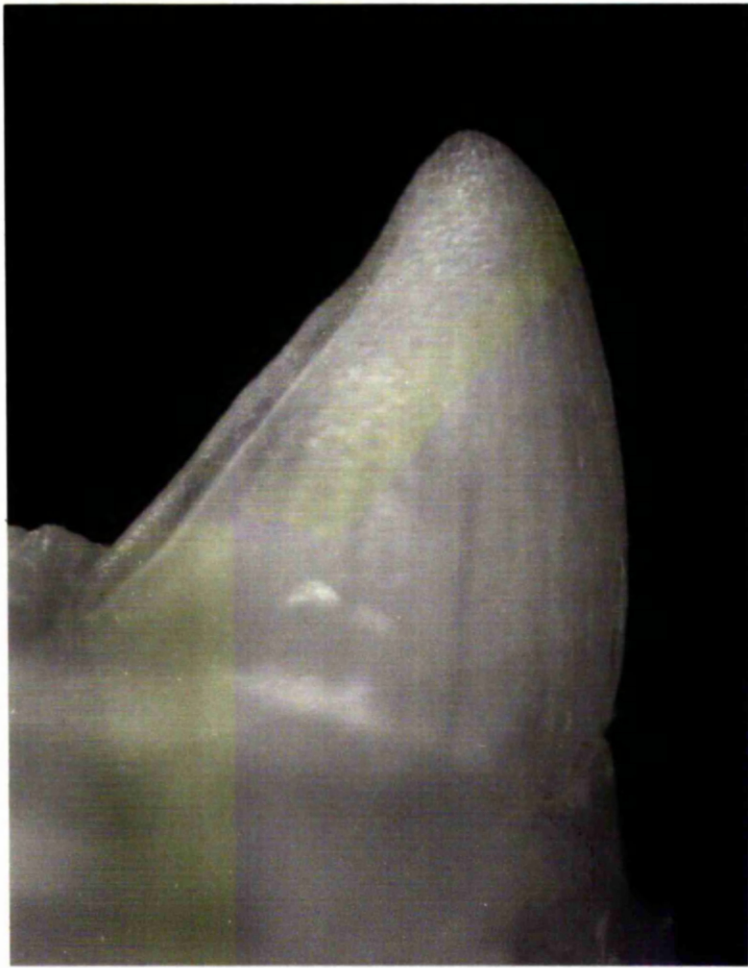


PLATE 3

Dissection photograph showing the fourth youngest leek leaf developing inside the 'sheath', seen under a stereo microscope (x10 eyepiece, x1.7 zoom lens).

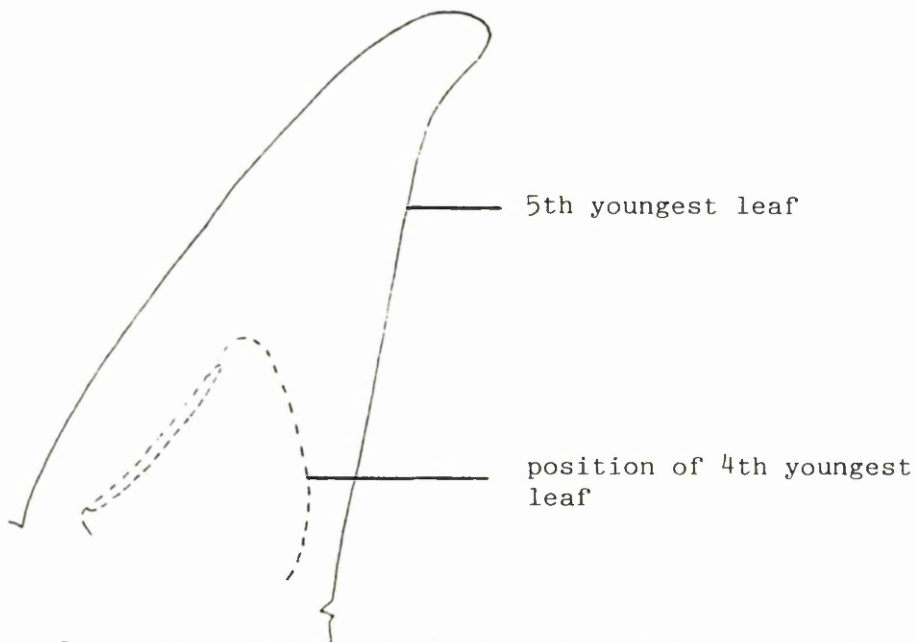


PLATE 4

Dissection photograph showing the fifth youngest leek leaf developing inside the 'sheath', seen under a stereo microscope (x10 eyepiece, x1 zoom lens).

4.2 Leaf Development and Expansion in the Leek

Many of the results presented in the following sections have been published elsewhere (Hay & Brown, 1988).

4.2.1. **Leaf Initiation and Appearance**

For each sowing of Experiment 2, including transplants, linear regression analysis showed that there was a close linear relationship between accumulated temperature above 0°C since sowing and the number of appeared leaves per leek stem (Table 1). The number of leaves appearing per 100°C days was similar for all the sowings, including the transplants, with a significant decline only at the third sowing. However, the number of leaves appearing was considerably greater in 1983 (data of Hay & Walters), when warmer and drier growing conditions were experienced (Channon & Kirkwood, 1984). This suggests that differences in environmental factors between seasons may affect leek leaf appearance more than those between sowings in a single growing season.

TABLE 1

Characteristics of the linear relationships between leek leaf appearance and accumulated air temperature (screen, > 0°C) since sowing.

Sowing Date	Number of leaves appearing per 100°C days \pm S.E.	r	Daylength ¹ , h, min (rate of change of daylength, h day ⁻¹) at crop emergence.
<u>1983</u>			
12 April	0.92 \pm 0.019	0.996	15.30 (0.07)
<u>1985</u>			
19 April	0.77 \pm 0.018	0.996	16.03 (0.06)
3 May	0.72 \pm 0.022	0.995	16.33 (0.06)
17 May	0.60 \pm 0.024	0.992	17.21 (0.03)
4 March (transplanted)	0.74 \pm 0.037 ²	0.988	16.00 (0)

¹ = data from Smithsonian Meteorological Tables.

² = calculated from field measurements after transplanting.

The data from the destructive sampling of experiment 1 (sowing 2) showed that there was also a linear relationship between accumulated temperature and the total number of leaf primordia initiated by the stem apex ($r > 0.99$) (Figure 5). However, the rate of leaf initiation was faster than that of leaf appearance (1.00 primordia per 100°C days compared with 0.76 leaves per 100°C days). It is interesting to note that the latter value is slightly higher than that of 0.72 in Table 1, for non-destructive measurements of sowing 2. Clearly, destructive sampling allows greater precision in the identification of leaves. Figure 5 also shows that leaf primordia did not accumulate on the apex, with primordia remaining at 2 per apex throughout vegetative growth of the leek. Only once floral primordia were initiated (early November) did accumulation at the apex take place.

Figure 6 shows that pseudostem height also increased linearly with accumulated temperature (0.26 cm per 100°C days, $r > 0.86$), where this measurement is analogous to the pseudostem of cereal plants (Kirby & Appleyard, 1984; Hay, 1986). However, as indicated earlier, crowding of leek leaves near the ligule of the youngest fully-expanded leaf occurs as the growing season progresses. This means that a newly emerging leaf tip may have to travel slightly further than the so called pseudostem height in order to appear. Thus, the values in Figure 6 where accumulated temperature is greater than 1400°C days since sowing (ie.

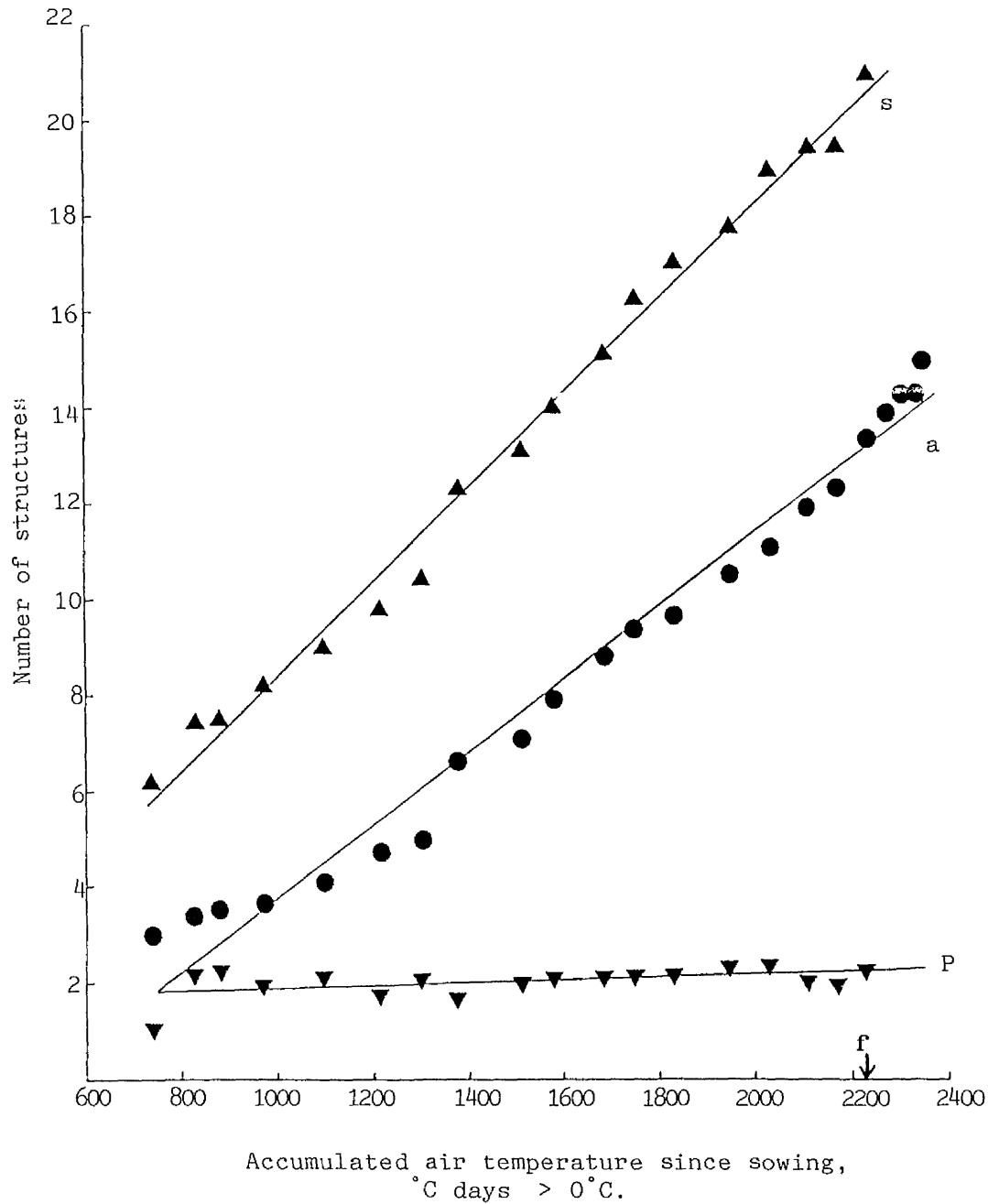


FIG 5

Changes with accumulated temperature in (s), the total number of structures initiated, (a) the number of appeared leaves, and (p) the number of primordia on the stem apex, of a leek plant, 2nd sowing. f indicates the start of primordia accumulation and floral development. Lines fitted by linear regression analysis of data from ten plants per sampling date.

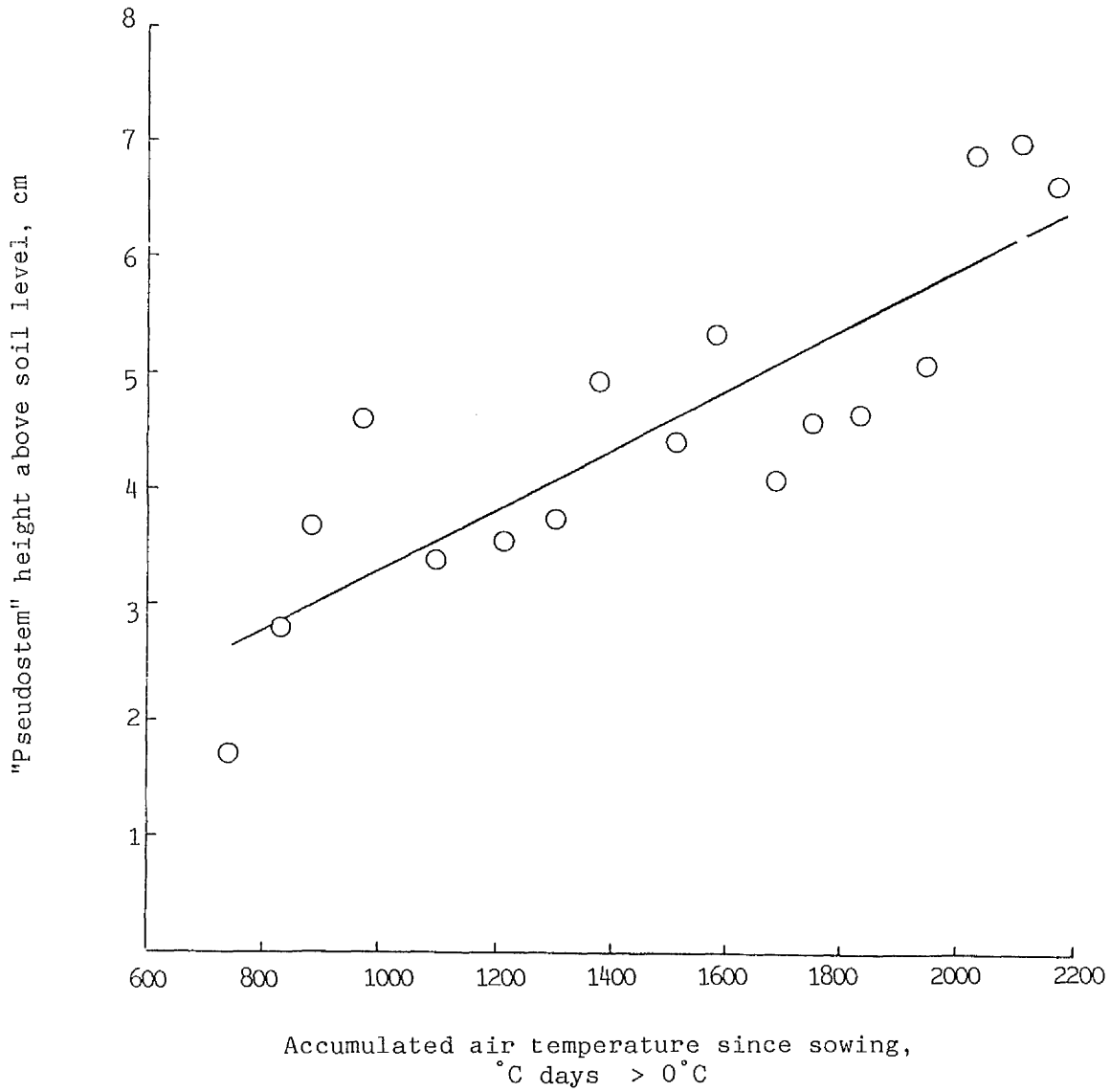


FIG. 6 Changes with accumulated temperature in "pseudostem" height above soil level of a leek plant, 2nd sowing. Line fitted by linear regression analysis of data from ten plants per sampling date.

when the number of appeared leaves exceeds 6) are not as accurate since they represent strictly the height of the youngest ligule above the soil surface (as in the case of cereals). There may be as much as a further 1 cm for a leek leaf to travel in order to appear past other expanding leaves. It is, therefore, advisable not to use the term pseudostem to describe leek plant development.

Examination of results from 1983 (data of Hay & Walters) showed that the distance from the apex to the point of appearance was measured. This increased linearly with accumulated temperature (1.28 cm per 100°C days > 0°C, $r > 0.98$). This indicates that the distance to the point of appearance also increased linearly with leaf number. It is assumed that the same inter-relationships existed in the 1985 plants.

Making this assumption about sowing 2 plants in 1985; and knowing that successive leaves were initiated at intervals of 100°C days (the plastochron, P_1) and appeared at a constant phyllochron (132°C days, P_h) (Figure 5), in spite of the fact that the distance to be travelled by the leaf tips increased progressively, it is possible to explain what was happening in the leek leaf system. There was a linear relationship between accumulated temperature and both leaf initiation and 'sheath' extension, with no accumulation of primordia at the apex. Therefore, the additional (equal) distance (D) which each

successive leaf tip travelled (at extension rate R) took the same amount of accumulated temperature (32°C days). This can be expressed in simple mathematical terms as:

$$P_h = P_1 + D/R$$

where the constants of P_1 , R and D are expressed in terms of accumulated temperature.

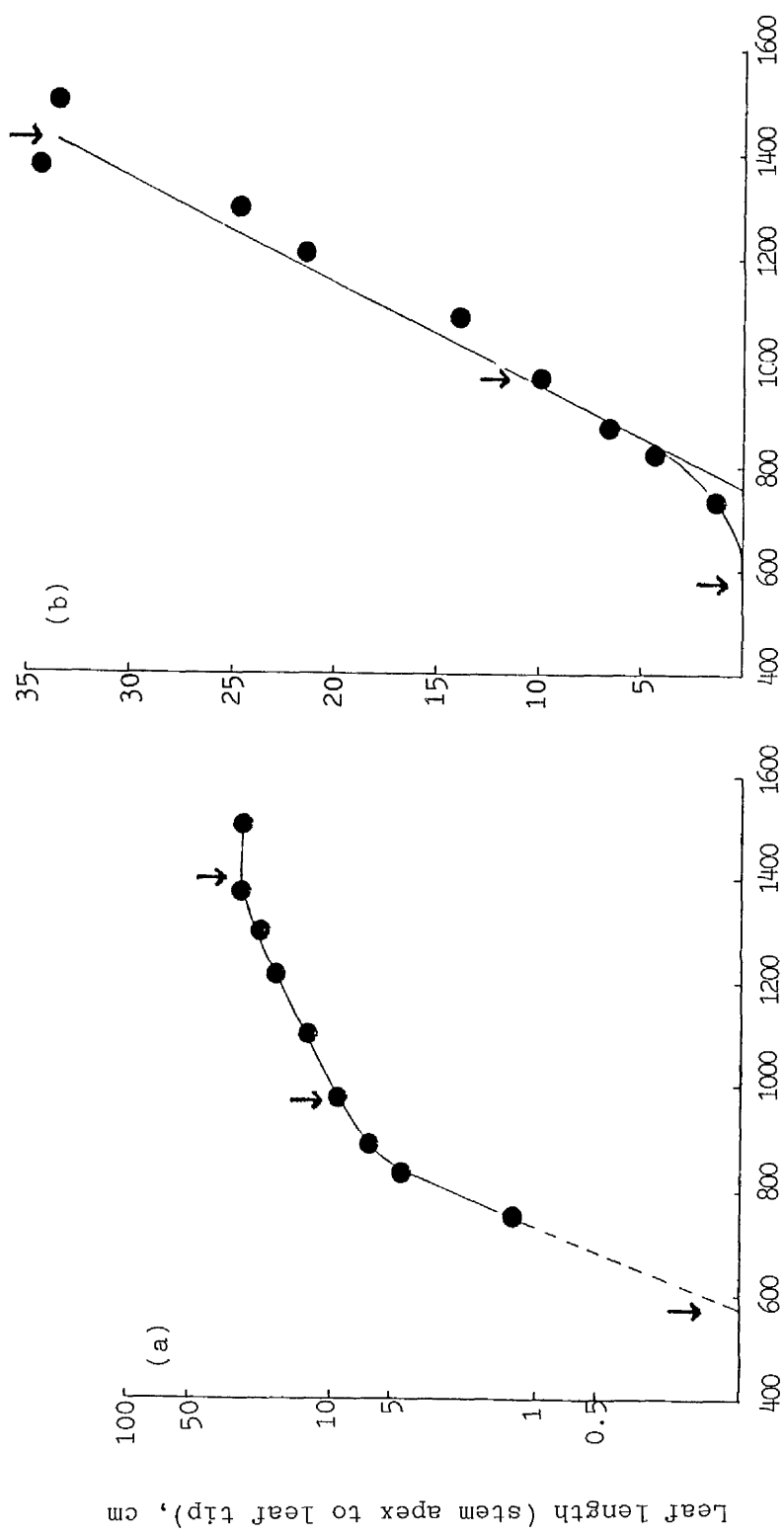
It can be concluded that the regular appearance of leek leaves is a consequence of the co-ordinated response to accumulated temperature of leaf initiation and 'sheath' extension, with no need for acceleration of the rate of extension of successive leaves.

4.2.2. Leaf Expansion Before and After Leaf Appearance

Leaf extension zone measurement was carried out on intact leek plants with 10 or 11 appeared leaves (see Section 3.6.2). Dissection of the plants showed that for leaves which were still expanding (ie. leaves 8-12), extension was restricted to the zone 3-4 cm from the apex, where the distance between needle pierce marks had increased during a 48-hour period. Leaf tissues above this zone were fully expanded, since the distance between needle pierce marks remained constant. Whether leaves had or had not appeared, the length of extension zone did not

seem to vary, and no relationship could be found between the length of the zone and the length of the leaf sheath. Overall, there was no evidence that the length of the extension zone varied consistently from leaf to leaf.

Sequential destructive harvesting and dissection of plants allows analysis of the full time course of leaf extension to be made, including the phase before leaf appearance. However, this procedure often gives highly variable results. Gallagher (1979) found this when using highly uniform plants of cereal varieties. Since leek varieties are more variable than cereals this effect is intensified. However, by choosing representative plants carefully, the pre- and post-emergence extension of leaves 4, 5 and 6 of sowing 2 could be reconstructed. Figure 7a shows that the relative rate of leaf extension had decreased considerably by the time that the leaf tip was visible, but leaf extension during the post-appearance phase accounted for approximately 70 per cent of the final leaf length. Plotting leaf length against accumulated temperature as a simple plot (Figure 7b) showed that, after a relatively short lag phase, leaf extension can be described by a linear relationship similar to that found for cereals (Gallagher, 1979). Linear regression for leaves 4, 5 and 6 gave rates of leaf extension of 529,581 and 526 μm per $^{\circ}\text{C}$ day respectively. This tends to confirm that rates of leaf extension are effectively the same for successive leaves.



Accumulated air temperature since sowing, °C days > 0°C

FIG. 7 Semilogarithmic (a) and simple (b) plots of the time-course of the extension of leaf 4, 2nd sowing. The three arrows indicate primordium initiation, leaf appearance and the achievement of full leaf extension, respectively.

Since leaf tip appearance coincided with the start of the linear phase of extension, in leaves 4, 5 and 6, it was possible to use the non-destructive measurements of successive leaves also, to investigate the relationship between leaf number and the rate of leaf extension. These data were much less variable than results from destructive sampling because the same leaves were measured on several occasions throughout the growing season. The rate of extension was found to be effectively the same for successive leaves of the plants of any particular sowing (Table 2).

TABLE 2

Rates of extension of leek leaves during the linear phase, from non-destructive sampling of twelve uniform plants per sowing. Rates are means \pm S.E.M.

Sowing	Leaf Number	Rate of Extension cm (100°C days) ⁻¹
1	5	8.4 \pm 0.83
	6	8.5 \pm 0.61
	7	8.5 \pm 0.30
2	5	8.0 \pm 0.42
	6	8.9 \pm 0.35
	7	7.8 \pm 0.31
3	4	5.6 \pm 0.72
	5	5.7 \pm 0.39
	6	6.4 \pm 0.35
Transplanted	8	6.2 \pm 0.35
	9	5.8 \pm 0.26
	10	6.5 \pm 0.26
	11	6.7 \pm 0.28
	12	5.8 \pm 0.26

Only the following differences are significant at $P < 0.1$: sowing 2, leaf 6 vs. leaf 7; transplanted leaves 9, 12 vs. leaves 10, 11. All other differences are not significant.

4.2.3. Ontogenetic Trends in Leaf Dimensions

The dimensions of fully-expanded leaves from sowings 1, 2, 3 and transplanted leeks tend to conform to a simple ontogenetic trend (Figure 8), as found in other investigations (eg. Bonnet, 1976b). The small but significant differences between sowing and planting methods, towards the end of curves, were possibly caused by very low temperatures occurring in November (mean daily temperature of 3.5°C). In general, there was a progressive increase in the length of successive leaves.

The phyllochron (for leaf tip appearance) remained constant throughout the growing season in terms of accumulated temperature (132°C days), but the number of leaves per plant which were expanding at the same time increased progressively. Indeed, by November a single plant had as many as 10 expanding leaves, which varied in length from 3 mm to 45 cm or longer. This suggests that, since the rate of extension of leaves remained the same, the duration of extension increased progressively, resulting in the progressive increase in the length of successive leaves. This is confirmed by the fact that 'sheath' length increased linearly with accumulated temperature and leaf number, and by the ontogenetic trends in leaf dimensions.

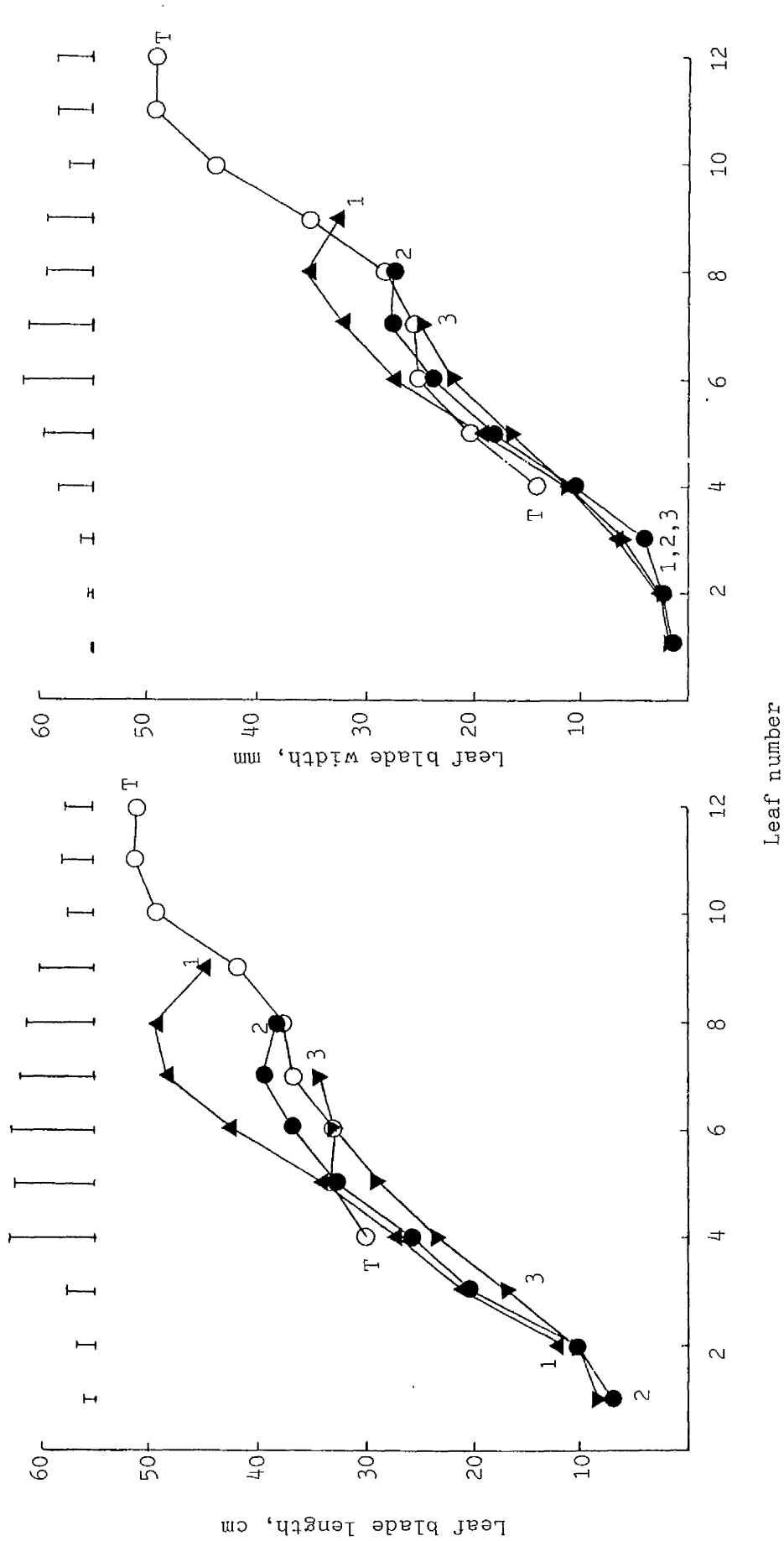


FIG. 8 The dimensions of fully expanded leaves of plants from sowings 1, 2, 3 and transplanted leeks (T), 1985. The vertical bars indicate 2 x S.E.M.

4.3 The Effects of Rust Disease on Leek Growth and Development

4.3.1. **Disease Development**

In the rust-infected (R) subplots of experiment 3, plants were inoculated during the week 29th July to 2nd August. By 26th August, infection exceeded 5 per cent, and by 21st October 10 per cent. The highest recorded incidence was 17 per cent of total canopy area on 2nd December.

The healthy (H) plants were protected from rust infection by spraying with fungicide. This treatment began before the plants were exposed to infection and, after the appearance of the first visible symptoms of infection (24th September), held the level of infection below 1 per cent until the beginning of October, and below 5 per cent to the end of the experiment (17th December).

The sprayed (S) subplot was treated in the same way as H subplot. However, these plants must have been exposed to natural infection earlier than H subplots because the date of visible infection (26th August) was about four weeks earlier than that of H subplots. It would appear that the stand was already infected by the time of the first spray. However, fungicide treatment held infection levels to below 1 per cent throughout September, and to approximately 5 per cent up to the end of the experiment.

In the unsprayed (U) subplot the pattern of rust incidence was generally similar to that of the S plants, although the level of infection was slightly higher at each date. The 5 per cent level was achieved one week earlier and the affected area exceeded 10 per cent from late October.

Thus, rust disease developed in all the subplots, and in two ways: by artificial inoculation (R) and by natural infection (H, S and U). The timings and levels of infection in R and U plants were representative of natural rust infection of leeks in SW Scotland.

4.3.2. Leaf Area Index

Leaf area index (LAI) is a crop-orientated concept of leafiness in relation to land area. It can be used as a broad index of the ability of the stand to intercept solar radiation (Hunt, 1978).

In general, leaf area indices for the various leek canopies were low. This can be explained partly because of the wide spacing of plants (25 m^{-2}), and because of the slow growing nature of plants. Another important factor was that 1985 was noted as an exceptionally poor growing season (Walker & Kirkwood, 1986).

The seasonal patterns of leaf area index are shown in Figure 9, for healthy (H), rust-infected (R), sprayed (S) and unsprayed (U) plants. A delay in infection of H

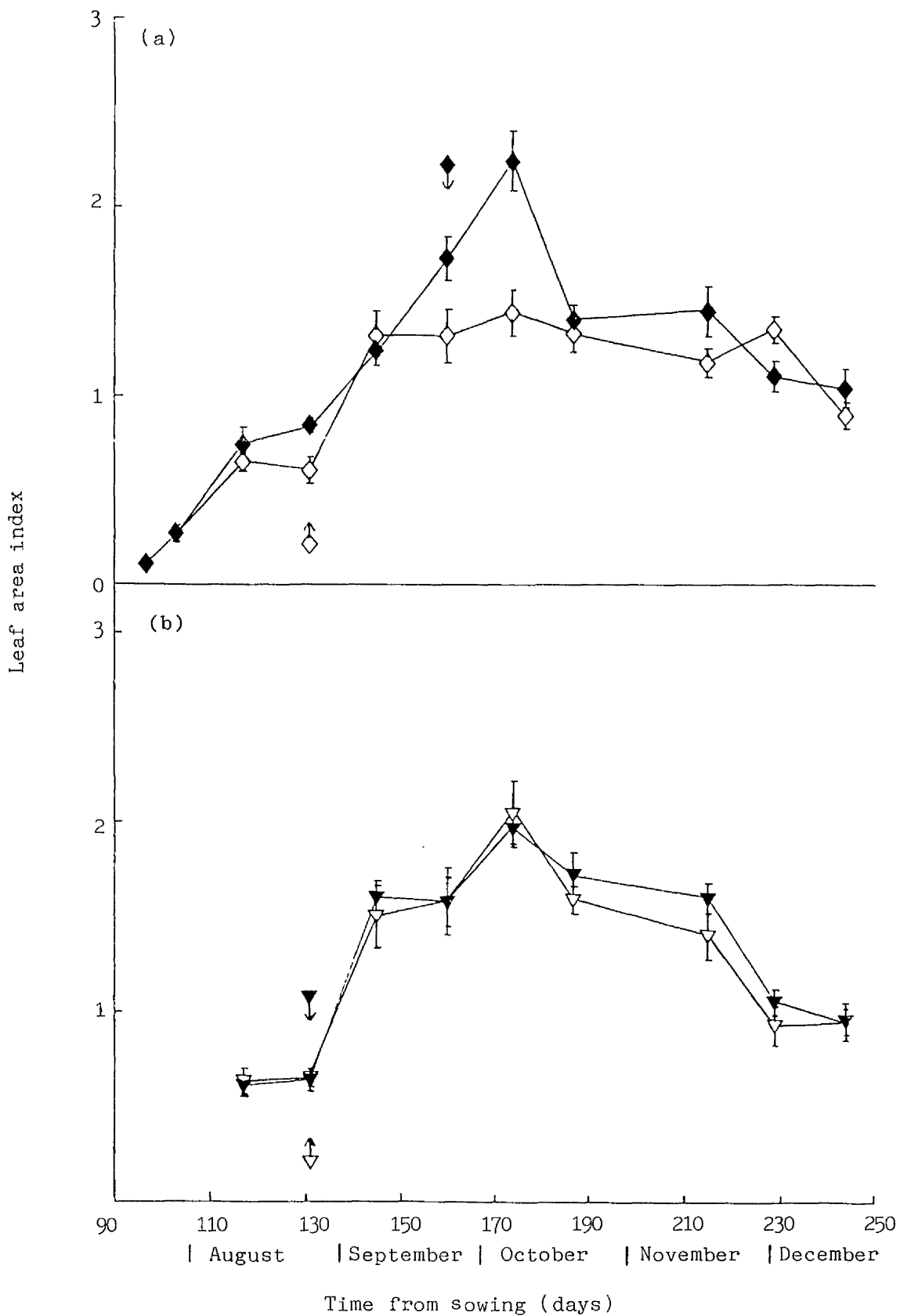


FIG. 9 Changes in leaf area index (LAI) of (a) healthy (◆) and rust-infected (◇) leek plants, and (b) sprayed (▼) and unsprayed (▽) leek plants. Points represent data from ten plants and the vertical bars indicate \pm S.E.M. The arrows indicate first visible signs of infection.

plants relative to R plants (Figure 9a) was associated with a higher LAI over some 20 to 30 days, from late September to early October. However, once the H plants had become infected, it took about 15 days for the leaf area index to begin to fall, to almost that of the R plants. After this fall, differences between treatments were smaller. Differences in leaf area index between S and U plants (Figure 9b) were smaller and only significant towards the end of the experiment (late October/early November), when the sprayed canopy had higher leaf area indices for about 20 days.

4.3.3. Components of Leaf Area Index

Figure 9 provides evidence of a depression in leaf area index associated with rust infection. Each component of canopy expansion (leaf appearance, expansion and senescence) was examined to investigate the cause of leaf area index depression.

The number of appeared leaves for H and R plants, at weekly intervals from 7th August to 12th November, were almost identical. This was confirmed by linear regression analysis, which showed the mean rate of leaf appearance to be 0.60 per 100°C days > 0°C for H plants and 0.61 for R plants. These compare favourably with the mean rate of 0.60 for the third sowing at Templefield, which was sown at the same time as the Diamondfield plots, and showed minimal symptoms of rust infection. It can be

concluded that the rate of leaf appearance was unaffected by rust infection.

Measurements of the length of visible green lamina, from tip appearance to full expansion (eg. for leaf 6, Figure 10) indicate that the rate of leaf expansion was also unaffected by rust infection. From day 112 to 149, the lengths of lamina were almost identical for H and R plants. Thereafter, rust infection appeared to accelerate senescence, with a more rapid decline in green leaf length occurring compared to H leaves. Complete senescence was brought forward by about 20 days.

Dimensions of fully-expanded leaf laminae were compared (Table 3), showing that lamina size was similar for H and R plants up to leaf 7, at least. This indicates that the duration of leaf expansion was not reduced by infection.

TABLE 3

Ontogenetic trends in the dimensions of fully-expanded leek laminae (means of ten plants).

Leaf Number	Laminar Length, cm (+ SEM)		Laminar Width, mm (+ SEM)	
	Healthy	Rusted	Healthy	Rusted
4	26.4 ± 0.89	25.9 ± 1.69	13.7 ± 10.63	13.4 ± 1.03
5	30.2 ± 1.72	30.4 ± 1.73	18.1 ± 0.96	18.7 ± 1.28
6	37.2 ± 2.06	35.3 ± 1.19	22.8 ± 1.18	23.5 ± 1.08
7	38.8 ± 2.16	36.1 ± 1.54	25.6 ± 1.42	26.2 ± 0.81
8	40.4 ± 2.41	34.3 ± 1.79	28.7 ± 1.79	26.5 ± 1.10

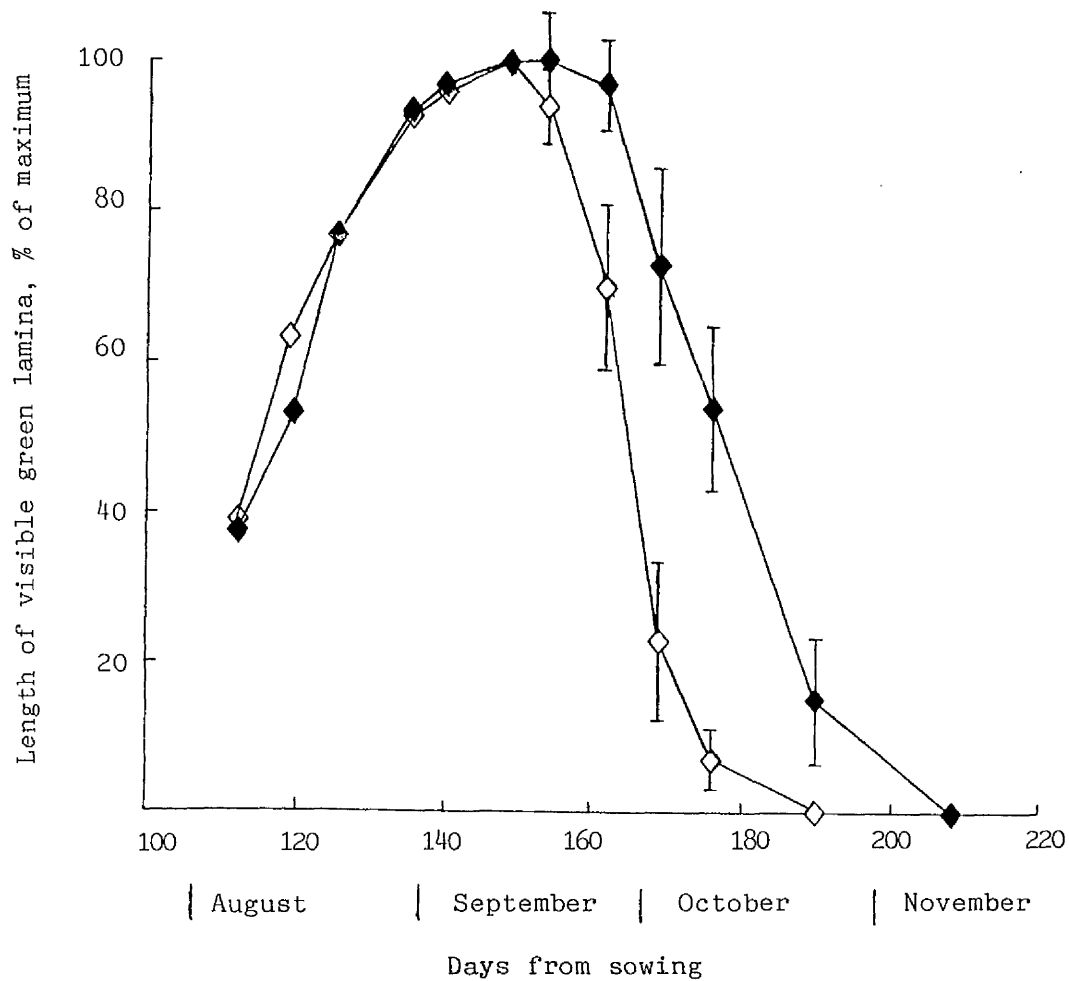


FIG. 10 The extension and senescence of the sixth leaf of healthy (◆) and rust-infected (◇) leek plants. Values are means from the same ten plants at each sampling, and the vertical bars indicate \pm S.E.M.

Thus, leaf area generation appeared to be unaffected by the level of rust infection experienced during the course of the experiment. The reduction in leaf area index shown by the rusted canopy in September and October was therefore a consequence of accelerated leaf senescence. Furthermore, detailed monitoring of the decline of green leaf length of each leaf showed that later leaves of R plants senesced more rapidly than did those of H plants. This is shown for leaf 6 (Figure 10) and leaf 7 (Figure 11).

Inoculation with rust (in early August) did not affect leaf appearance and expansion, but shortened leaf life span. As a result, a significant reduction in leaf area index was not caused until mid-September, when the "healthy" canopy began a short-lived superiority over the "rust-infected" canopy. This came to an end in late September, when the first visible symptoms of rust on the "healthy" plants could be seen. The leaf area index of "healthy" plants began to fall, reaching the "rust-infected" level by mid-October.

In the case of the plot with "sprayed" and "unsprayed" plants, the rates of leaf appearance, expansion and senescence were the same for the two treatments, as were the time courses of leaf area index up to mid-December.

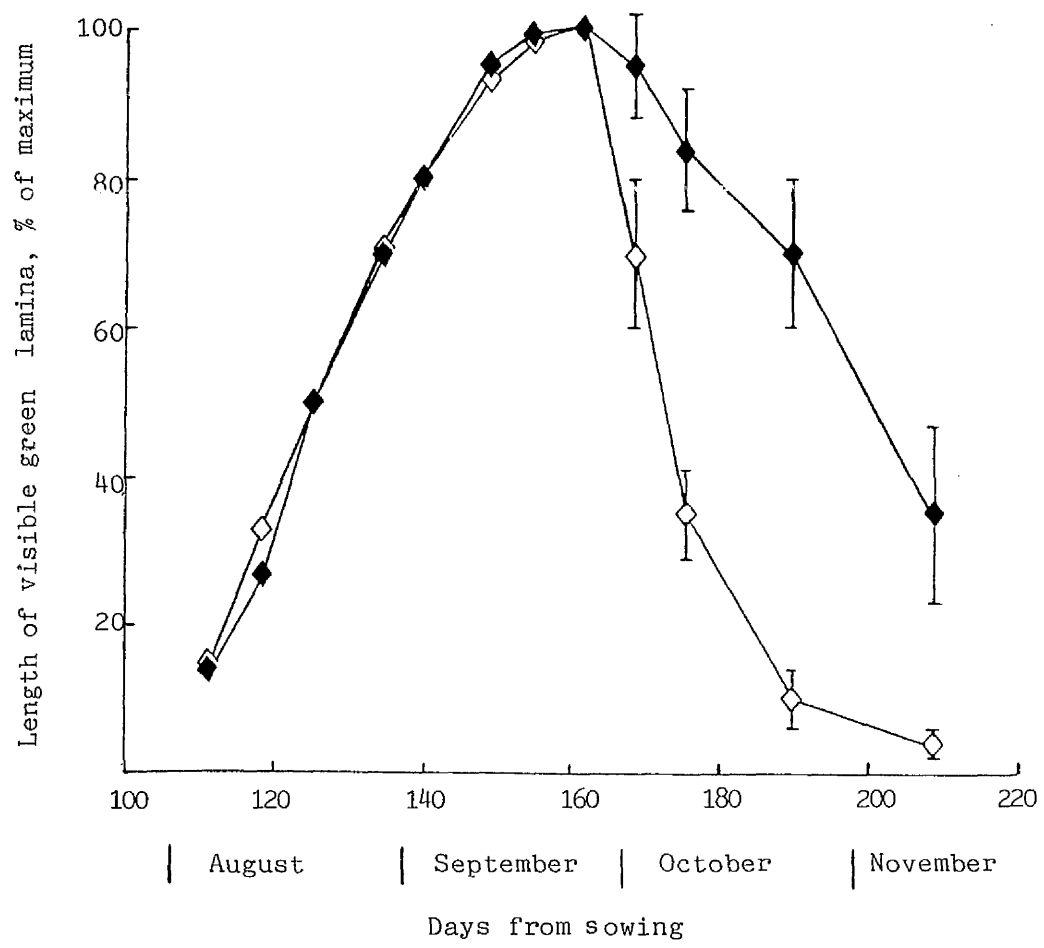


FIG. 11 The extension and senescence of the seventh leaf of healthy (◆) and rust-infected (◇) leek plants. Values are means for the same ten plants at each sampling and the vertical bars indicate \pm S.E.M.

Note added after binding:

In all cases, the general fall in NAR with time can be related to a general fall in monthly radiation totals (Figure 1) over the growing season.

Although it has been suggested that differences in NAR between treatments were due to changes in photosynthetic efficiency, it should be stressed that reduction in net photosynthesis may be the result of loss of material by enhanced respiration or senescence, in addition to changes in the activity of the photosynthetic apparatus. It should be noted that it is difficult to identify accurately times when the effect of rust was first apparent, since curve-fitting growth analysis smoothes transitions from one phase of growth to another.

4.3.4. Photosynthetic Efficiency

Curve-fitting growth analysis (Hunt & Parsons, 1974) was used to estimate mean canopy net assimilation rate for H, R, S and U plants (Figure 12). Thus, the overall net photosynthetic efficiency of each canopy could be assessed. Figure 12a shows that at the initial harvest, the rusted plants had a lower net assimilation rate than did healthy plants. At this time there were no visible signs of infection. However, it would appear that infection was affecting the photosynthetic efficiency of plants. By the time that infection was visible, the difference between net assimilation rates had become smaller, as rates fell in both healthy and rust-infected plants. The progressive infection of healthy plants was also associated with a fall in net assimilation rate after 150 days from sowing. Levels were lower than those of the rust-infected canopy from 150 to 200 days.

Figure 12b shows that because sprayed and unsprayed plants were probably already affected by rust at the start of the spray program, a depression in net photosynthesis had already occurred by the time of the first growth analysis. However, the photosynthetic efficiencies of the two canopies were very similar, with the level for sprayed plants remaining only slightly higher than that of unsprayed plants.

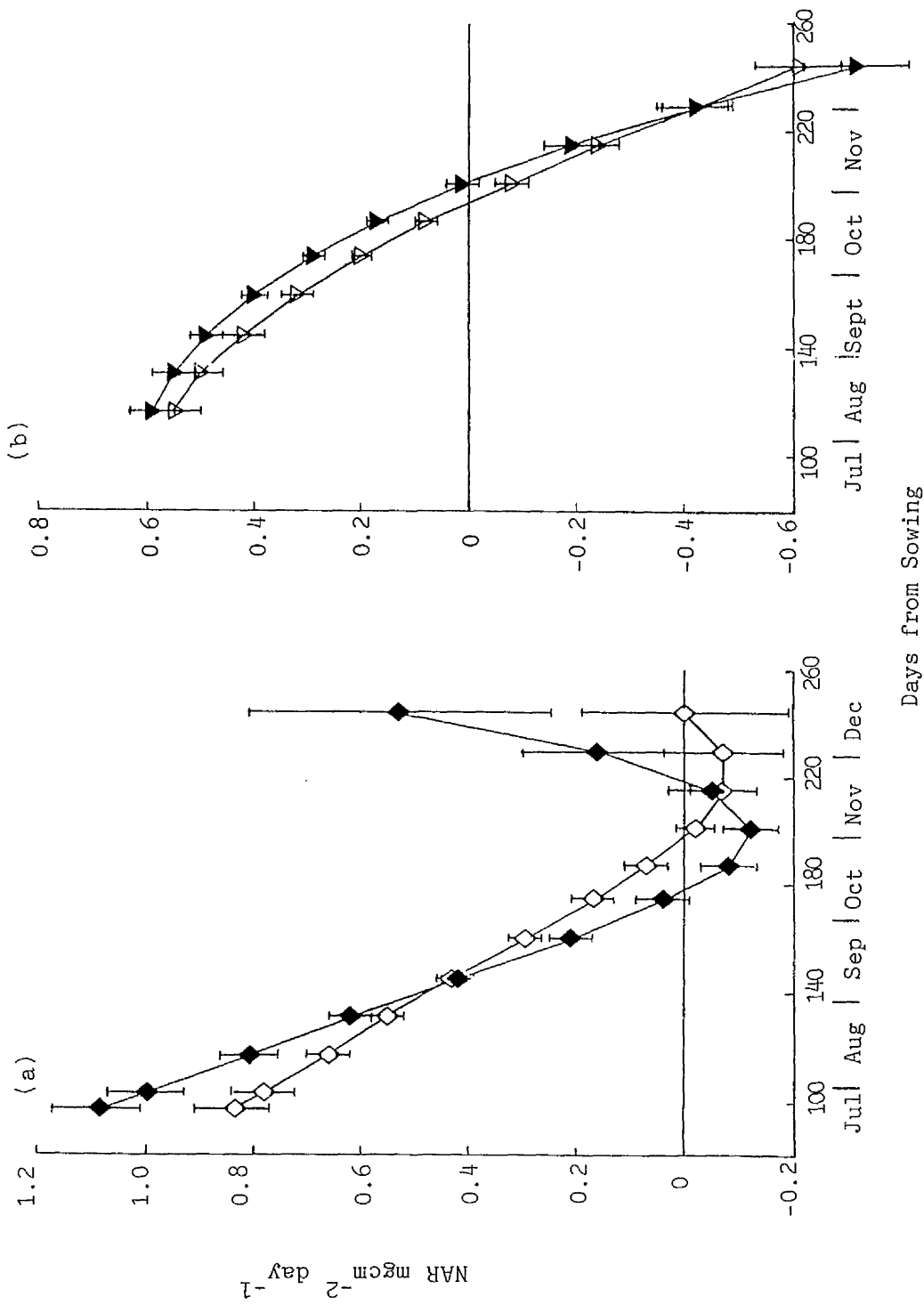


FIG. 12 Net assimilation rate (NAR) in (a) healthy (◆) and rust-infected (◇), and (b) sprayed (▼) and unsprayed (▽) leek plants. Values are derived from curve-fitting growth analysis of ten plants at each sampling, and the vertical bars indicate \pm S.E.M.

4.3.5 Dry Matter Production

Figure 13 shows that the biomass of each of the leek stands reached a maximum around the first week of October. These high levels were maintained until mid-November, after which a gradual decline occurred. These results are consistent with the decline in leaf area index (Figure 9) and the progressive fall in net assimilation rate (Figure 12). In the rust-infected plants, the depression of net assimilation rate during the first three weeks after infection resulted in a lower crop dry matter production, which continued until late November. The difference in leaf area index between healthy and rust-infected plants was less important since it did not occur until maximum biomass had been achieved.

It is important to note that results for sprayed (S) and unsprayed (U) plants, throughout section 4.3, suggest that chemical treatment of plants, with the fungicide Bayleton, had a negligible effect on leek growth and development. Therefore, the possibility that there may have been phytotoxic effects of the fungicide on healthy (H) plants can be ignored, where comparisons with rusted (R) plants are made. Indeed, triademefon, the active ingredient in Bayleton, has been shown to have no effects on yield or on green leaf area in field-grown spring barley and wheat (Lim & Gaunt, 1986).

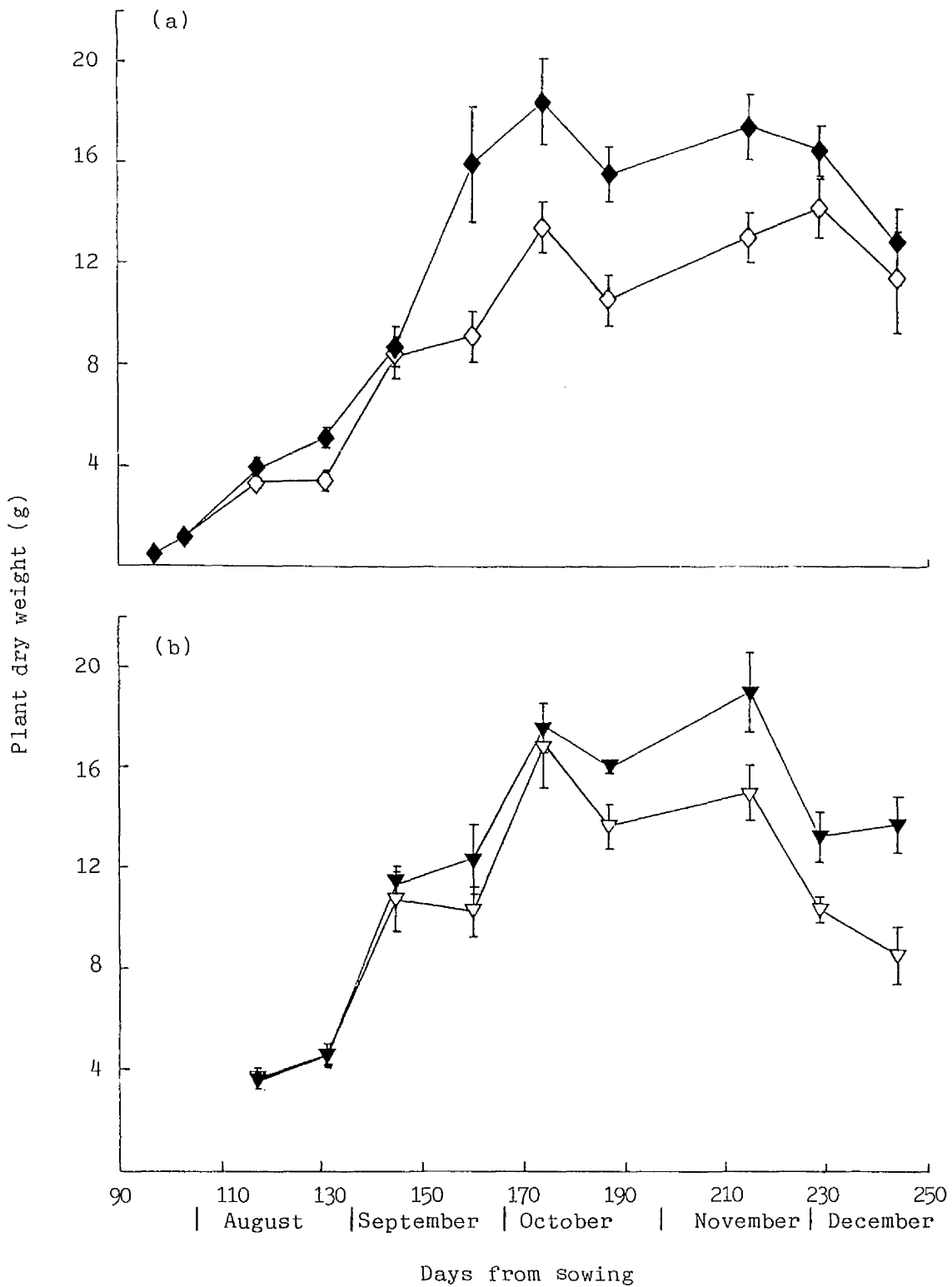


FIG. 13 Whole plant dry weight in (a) healthy (◆) and rust-infected (◇), and (b) sprayed (▼) and unsprayed (▽) leek plants. Values represent the mean of ten plants at each sampling, and the vertical bars indicate \pm S.E.M.

V DISCUSSION

5.1 Leaf Development and Expansion in the Leek

This research has shown that leaf development in the leek plant follows a relatively simple seasonal pattern. Initiation of leaf primordia occurs at regular intervals with respect to accumulated temperature (plastochron $100^{\circ}\text{C days} > 0^{\circ}\text{C}$). Following initiation, and for each leaf, a lag period exists, during which the rate of leaf extension increases to reach a constant value. Almost simultaneously the leaf tip appears, or becomes visible. Subsequent leaf appearance is governed by accumulated temperature, with equal increments of accumulated temperature being involved. It was also shown that the rate of leaf extension was identical for each successive leaf. However, as the plant ages, those leaves which are produced later have, by necessity, to travel a greater distance before their tips appear. This extra distance was found to increase linearly with increasing leaf number.

Taking all these facts into account, it was calculated that an additional 32°C days were required for each successive leek leaf, between initiation and appearance, which results in a phyllochron of 132°C days .

Furthermore, studies of leaf expansion, before and after appearance, revealed that the duration of the linear phase

of leaf expansion increased progressively with each successive leaf. Consequently, this led to leaves which were progressively larger, in terms of laminar length and breadth.

Overall, a relatively simple ontogenetic trend in leek leaf size became apparent. These findings contrast markedly with similar studies using other monocotyledonous crops, especially cereals.

The growth and development of cereal leaves presents a more complex system than that of the leek. This is largely due to the early onset of reproductive development, compared with the leek. Another important consideration is that although the vegetative apex remains below the level of the soil surface in both cereals and leeks, primordia accumulate on the apex in the former, but not in the latter. Cereal leaves have successively longer sheaths, and in some cases sheath extension can be linked to the reproductive stage of the apex (eg. in winter cereals).

Hay (1986) showed that an exponential relationship existed between pseudostem length and accumulated temperature, in winter wheat, barley and rye, whereas leeks maintain a linear relationship. In order to appear at regular intervals of accumulated temperature, each succeeding cereal leaf must extend further to pass the ligule of the

youngest fully-expanded leaf, so the rate of extension must increase with leaf number. Detailed work by Kemp (1980), using wheat leaves, showed there to be a progressive increase in the length of the leaf extension zone, although there was comparatively little change in the relative rate of zone extension. Consequently, the ontogenetic trend in cereal leaf size is affected by the progressive increase in the rate of leaf expansion, whereas successive leek leaves exhibit a progressive increase in the duration of leaf expansion.

However, the ontogenetic trends in cereal leaf size can show greater complexity. The flag leaves of many spring barley cultivars are relatively small (and contribute relatively little to final grain yield), with previous leaves having increased to a peak size and then declined again as maturity was approached. Wheat leaves also reach a maximum size, after which there is a progressive decrease in leaf size before the flag leaf appears, although this decrease is much less marked than in spring barley since the top three leaves (but particularly the flag leaf) contribute substantially (approximately 40 per cent) to final grain yield.

It can be concluded that the leek provides a relatively simple model system for leaf development in the absence of reproductive development, with a simple ontogenetic trend in leek leaf size occurring.

Whilst the base temperature used in this work (0°C) has allowed for assessment of events in leaf development, with linear responses having good correlation coefficients, it should not be overlooked that the base temperature for leek leaf development was assumed to be similar to that for cereals. 0°C has been used as a base temperature for cereal leaf development in a number of field studies (eg. Baker & Gallagher, 1983), with linear responses being produced. Other workers have used base temperatures near to 0°C, such that T_b can be said to vary from 0-3°C for most temperate cereal crops. However, it is interesting to note that recent work on winter wheat (Hay & Delécolle, 1989) has revealed several examples of bi-linear rather than linear responses when T_b is taken as 0°C. If this base temperature is varied data points can be compressed and linear relationships, with satisfactory r values, obtained. However, this may be correct mathematically, but true developmental phenomena may be obscured in efforts to present linear responses. Future work on leeks could involve better methods of establishing the base temperature for leaf development. Salter, Akehurst and Morris (1986) used a base temperature of 6°C for leeks, although they were studying the marketable yield of plants and not leek leaf development.

Environmental factors appear to influence cereal and leek leaf appearance in different ways. Baker, Gallagher and Monteith (1980) found that the rate of leaf appearance in

winter wheat (in terms of accumulated temperature) increased as the sowing date was delayed from October to March. It was shown that a significant correlation existed between the rate of leaf appearance and the mean value of daylength, during the time from crop emergence to flag leaf appearance. However, an additional June sown trial showed that despite the higher mean value of daylength, these plants did not exhibit the fastest rate of leaf appearance (as anticipated). Instead, the rate was similar to that for a sowing which emerged in mid-December, at which time there was a similar, and small, rate of change of daylength. Indeed, for all sowing dates, a strong correlation was shown to exist between the rate of change of daylength and the rate of leaf appearance. Therefore, it was postulated that the rate of change of daylength at crop emergence was the factor which controlled the rate of leaf appearance. Subsequent work has provided support for this hypothesis (Kirby, Appleyard & Fellowes, 1985).

In this study, the leeks in sowings 1 to 3 emerged over a relatively restricted range of rates of change of daylength, and their rates of leaf appearance were correspondingly similar. However, the rate of leaf appearance of transplanted leeks was indistinguishable from those which were direct sown, but the transplants were raised in a glasshouse where there was a constant daylength of 16 hours, and therefore a rate of change of

daylength of zero. It seems that the rate of change of daylength at crop emergence is not a factor controlling the rate of leaf appearance in leeks.

Field data from contrasting seasons (1983 and 1985) has shown that the rate of leaf appearance in leeks is not constant between seasons, even at the same site. In the dull, wet summer of 1985, the rate of leek leaf appearance was very much slower compared to the hot summer of 1983. Clearly, leaf development in the leek is not quantitatively similar from season to season. Conversely, Kirby et al. (1985) showed that leaf development for a particular wheat cultivar, and site, tended to be similar regardless of season.

It would appear that the co-ordination of leaf development in the leek is not controlled by environmental factors such as daylength, but by those which vary between seasons. Further field experiments could be designed to investigate possible controlling factors, such as solar radiation. Solar radiation totals over the growing season (April to November inclusive) showed a 5 per cent decrease in 1985, compared with 1983. In field experiments on the marketable yield of transplanted leeks, decreasing yields were associated with decreasing values of accumulated solar radiation, as well as with decreasing values of accumulated temperature (Salter, Akehurst & Morris, 1986).

5.2 The Effects of Rust Disease on Leek Growth and Development

Mild infection of field grown leeks was found to have little effect on the production of leaves, or their dimensions. However, it led to lower leaf area indices via accelerated senescence of leaves. Such reductions in leaf life span have been found in field experiments with other crop species and fungal pathogens. Relatively low levels of mildew (Erysiphe graminis) infection of spring barley did not affect the total amount of crop leaf area produced, but reduced canopy duration by accelerated senescence (Simkin & Wheeler, 1974; Jenkyn, 1976; Carver & Griffiths, 1981, 1982). Very detailed measurements of field-grown barley plants, mildly infected with the necrotrophic fungus Rhynchosporium secalis, have been carried out (Jackson & Webster, 1981). Small differences in the rates of leaf appearance were found, but the main effect of infection was accelerated senescence, which reduced leaf life span.

In contrast, Lim and Gaunt (1986) found that infection with mildew and leaf rust, of field-grown spring barley, led to reductions in leaf size, thereby reducing green leaf area at later growth stages. This resulted in large yield losses in the crop.

In glasshouse experiments more severe levels of infection can be obtained. These have been found to reduce canopy

development by delayed leaf appearance, smaller leaf laminae and reduced tillering. Such effects were shown in barley/mildew systems by Last (1962) and in wheat/yellow rust by Doodson, Manners and Myers (1964), causing substantial yield losses.

Infection of the leaves of a crop can cause reduced yield by affecting either the interception of solar radiation or the photosynthetic efficiency of the canopy, or by a combination of both effects.

If dry matter production is taken as a measure of crop yield, then rust infection was found to lower leek yields. Although infection caused a depression in leaf area index (via accelerated senescence), this occurred at a relatively late stage in the life of the crop, once maximum dry matter production had been achieved. Therefore, it would appear that the effect of rust on photosynthetic efficiency of leeks was by far the more important factor. Net assimilation was found to be depressed by rust infection in the field-grown plants, and this has also been found in laboratory experiments on glasshouse-grown leeks (Roberts, 1987). These experiments showed that infection with leek rust caused significant reductions in the net assimilation of leek leaves before the development of visible symptoms, with reductions in total dry matter yield in the order of 30 per cent occurring. Overall, reductions in total dry matter yield of rusted crops may result from

reduced net assimilation, rather than reduced interception of solar radiation late in the growing season.

These field investigations into the effects of rust disease on leeks were strictly of a preliminary nature; but, they provide some evidence of quantitative yield losses, in addition to deterioration in quality (appearance) of the leek. However, since infection eventually developed in all of the leek stands, it is not possible to assess the full long-term effect of infection upon crop production.

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