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FIFTY YEARS OF RYEGRASS RESEARCH IN NEW ZEALAND

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Abstract

Ryegrasses have dominated seed mixtures since the inception of pastoral farming in New Zealand largely because perennial ryegrasses are easily established, and persistent under a wide range of climatic and management conditions. Annual ryegrasses have vigorous seedling growth and can provide valuable high quality feed during the cool seasons. These virtues make ryegrass easily thk most important grass in New Zealand agriculture.

This review traces the history of ryegrass use and development form the early days of bush burn mixtures to the present day array of bred cultivars. Areas of research covered in the review include:

(1) The selection and breeding of cultivars
(2) Management effects on density and persistence
(3) Physiology (responses to light, temperature and mineral nutrition)
(4) Ryegrass diseases
(5) Ryegrass pests
(6) The ryegrass endophyte
(7) Ryegrass herbage quality

The concluding section examines the role ryegrasses are to play in diverse modern agricultural systems, and hence the goals for breeders.

INTRODUCTION

Research over the last 50 years reflects the importance of ryegrass to New Zealand pastoral farming. Sown pasture expanded from 3.5 million acres in 1918 to 18 million in 1960. Output has greatly increased, due not only to aerial topdressing and oversowing but also to improved efficiency of utilisation arising from increased understanding of what factors limit and promote growth.

Research was intiated in the 1920s by AH. Cockayne and Bruce Levy originally at the Biology Sectionof the Deptartment of Agriculture. They advocated care of pasture as a national asset, and the use of high quality seed on the first bush burn sowings. cockayne (1914) cautioned against the use of ryegrass on low fertility soils. Despite the diversity of soil types and climatic conditions, two grasses, perennial ryegrass and cocksfoot, were included in practically all sowings.

Between 1922 and 1923, Levy developed ‘Principles of Pasture Management’, advocating the use of the best ‘mixed pasture’ (grass and clover) seed available, and searching for the best management for optimum associations. His focus during the late 1920s, on fertility and soil moisture, led to his later conviction (Levy 1936) of the need to maintain a land environment conducive to a simple perennial ryegrass-white clover dominant sward.

With the establishment in 1928 of the Plant Research Station at Plamerston North, pasture grass testing immediately began revealing those strains with superior traits. Their purity and germination were protected through the Seed Certification Scheme, inaugurated in 1929 by J.W. Hadfield.

In 1968 ryegrass was included in all pasture mixtures (Harris 1968), and only during the last decade have alternative grasses and more complex mixtures received renewed consideration for permanent pasture (Lancashire 1978). Today’s market boasts eight varieties of Italian-type and nine varieties of perennial-type ryegrass, with more candidates under test. The bulk of the research behind these improvements compels examination by subjects, and exceeds the length limitations of these proceedings. The following digest will be accompanied by a full review which a has been submitted to the New *Zealand journal of* agricultural *research.*

(1) THE SELECTION AND BREEDING OF CULTIVARS

In the 1920s Levy and Davies (1929) studied the variation in available seedlines of the major pasture species. New Zealand had been largely self-sufficeint in seed since 1900 and different regional seed sources had reputations for the quality of seed. North Island perennial ryegrass seed was regarded as superior to that from the South (Cockayne 1914).

Levy showed that the best New Zealand lines of perennial ryegrass were superior in our environment to improted lines. In the 30-80 years of pasture species being in new Zealand, strains had evolved adapted to our climate and farming systems. Seed sources from arable regions, adapted to short rotations, tended to be stemmy, free seeding and short lived. Those harvested from well-managed permanent pasture were leafy, dense and persistent. Hawkes' Bay ryegrass was idenitifed as the best, and its identity was guaranteed under the Certification Scheme.

Levy found no good local Italian ryegrass lines, and so he selected from superior introduced material, and this was multiplied under the Certification Scheme for use in new Zealand.

Levy surveyed seedlines only available in commerce, and so did not study ryegrass populations from areas of permanent pasture where seed was not normally harvested. In particular, he did not study populations which had evolved in dairying districts.

Programmes of pedigree selection were begun within the best sources, and new superior foundation material was continually fed into the certification system (e.g. Corkill 1956). Hybridwere observed between Italian and perennial ryegrass and some rare plants combined the early vigour of the Italian, the leafiness of the perennial and intermediate persistence. These were augmented by crossing superior Italian and perennial ryegrass to breed short rotation ryegrass, released as H1 in 1943 (Corkill 1945). Backcrossing to perennial ryegrass and a selection programme led to the release in1965 of 'Grasslands Ariki' long rotation ryegrass (Barclay 1963).

H1 (later known as 'Grasslands Manawa') established rapidly and gave abundant, quality feed for up to 4 years under good conditions. Like Italian ryegrass, it has always been included in many permanent pasture mixtures (Harris 1968). Ariki ryegrass proved to be effectively perennial in good ryegrass country, and its growth was higher in quality and better spread through the year than 'Grasslands Ruanui' perennial (Barclay 1963; Bascand 1963).

During the 1950s, artificial tetraploids were induced in the major ryegrass populations studied in New Zealand. Tetraploids in general have larger leaves, tillers and seed and a lower dry matter content. 'Grasslands Tama' wester-wolds ryegrass was selected and released in 1968, providing a high-yielding winter greenfeed (Barclay & Vartha 1967). 'Grasslands Moata' Italian ryegrass has proved to be faster establishing than 'Grasslands Paroa', and as strong in the second year (Armstrong 1981). A tetraploid selected from Ariki, designated G4708, has been under test for many years, and is to be released next year. It is not as persistent as Ariki, but has higher growth potential and will fit into the short rotation role.

Ongoing interest in old pasture ecotypes intensified in the 1960s and from the Mangere population (Corkill et *al.* 1981) were bred 'Grasslands Nui' and 'Ellett'. These cultivars, released as adapted to dry conditions, have proved to be higher yielding under most conditions, and more tolerant of crown rust, than Ruanui. However, many of the yeild comparisons were no doubt confounded by different levels of infection with endophyte.

More recent developments from old populations have been 'Concord' (Waikato), 'Takapau Persistor' and 'Droughtmaster-' (Hawke's Bay) and 'Marathon' (Canterbury) (G. Rys 8 AV. Stewart, pers. comm.). However, since most sowings in New Zealand since the 1930s have been of pedigree seed, it is likely that these last four cultivars are related to Paroa or to Ruanui.

A collection of perennial ryegrassfrom hill country showed variation within sites but little in-site mean. There was no characteristic hill country type (Forde &

Suckling 1980). Overseas cultivars are continually tried in New Zealand, but have not proved satisfactory (Rumball & Armstrong 1975). Recently, cultivars have been imported specifically for multiplication and re-export.

Natural populations from old pastures in south Europe, particularly north west Spain and Portugal, have proved valuable in improving cool-season growth of New Zealand pasture plants, including the ryegrasses.

Disease resistance is a common theme in plant breeding world wide, and was a major element in the breeding of Ariki (Barclay 1963). Part of the success of 'Concord' and 'Yatsyn' can be attributed to their superior resistance to crown rust (see Easton et al. 1989).

Wilson (1971, 1975) selected within perennial ryegrass for a number of morphological and physiological traits possibly associated with efficiency of photosynthesis and water use, and with plant quality. Evans (1967) showed that perennial ryegrass had higher leaf tensile strength than other grass species tested, including Italian and hybrid ryegrass. Variation was associated with cellulose and sclerenchyma content, within species but not between. Wilson (1965) developed contrasting lines of Ariki in the hope that lower leaf strength, and associated low cellulose content, would improve animal performance, as suggested by Bailey (1964). Lancashire & Ulyatt (1975) found lamb growth rates to be marginally greater, but the trial was seriously confounded by endophyte levels (Lancashire et al. 1977). The low leaf strength line is high yielding, resistant to crown rust and grows animals well even with a high level of endophyte. Designated G33, it is to be released in 1989.

The shear strength of ryegrass is the subject of recent study (Easton 1989). However most interest in recent years has centred on persistence rather than quality.

(2) MANAGEMENT EFFECTS ON DENSITY AND PERSISTENCE

The management of pastures required adapting to the vigour of H1 ryegrass (Brougham 1954 a, b), and lower sowing rates were recommended. Persistence was enhanced by avoiding intense summer grazing (Brougham 1970).

Manawa suppressed Ruanui unless grazing was very intense (Harris & Thomas 1970), and it was contended mixtures were of no advantage as the weaker component left room for weeds. Prestidge *et al.* (1986) argued that susceptible species in a mixture harbour Argentine stem weevil which then attacks the perennial. However Percival et a/. (1989) found 'Ellett' and 'Concord' ryegrasses grew well together. Competition between ryegrasses and other species varied with cultivar, management and environment (Harris & Thomas, 1972; Harris *et al.* 1980; Cosgrove & Brougham 1985).

A ryegrass sward is a population of competing tillers, and establishment of new tillers is affected by management and by environment (Hunt & Field 1978; Korte et al., 1984). Tiller density is greater under frequent cutting or grazing than under a lax regime. Tiller initiation and death follows a seasonal rhythm, with numbers increasing in spring before and after reproductive development. Death is also high at this time so turnover is accelerated by nitrogen (Hunt 8 Mortimer 1982). Chapman et al. (1983) showed tiller density of a hill sward to be higher under set-stocking than rotational grazing. Leaf extension rates offset this difference so that total leaf production was the same.

(Edmond 1963) showed that treading has a detrimental effect on the growth of pasture, especially when the soil is wet, through reducing the vigour and/or the density of tillers, and through damaging roots. Soil type and vegetation cover (Brown 1968) influenced the effect. Of the species tested, perennial ryegrass was the most tolerant of treading. Short rotation ryegrass was sensitive during the summer, but was less so in winter when it is of most value.

With the production of new ryegrass cultivars, many trials have compared cultivars in different regions. Harris et *al.* (1977) showed Nui to be superior to Manawa, Ariki and G4708 over four sites, and to survive drought well. G4708 showed up as the best winter producer. Lancashire et al. (1979) and Goold (1982a, b) summarised a number of experiments, although many results must be confounded with endophyte level. Alternative species are proposed, high endophyte seed sources are recommended (Goold 1984; Thorn et al. 1987), despite the known effects on animal performance, and new cultivars are marketed in terms of their persistence and drought tolerance.

Several authors have shown newer cultivars to outperform old, particularly in having a better seasonal spread of growth (Barclay 1963; Harris 8 Johnson 1973: Harris et al. 1977; Baars et *al.* 1976; Hunt & Mortimer 1982; Goold 1982; Percival & Duder 1983). Vartha (1975) showed the drought resistant 'Media' ryegrass from Australia to be summer dormant and inferior in total production to Ruanui or a local persistent ecotype in Canterbury.

(3) PHYSIOLOGY (RESPONSES TO MINERAL NUTRITION, LIGHT AND TEMPERATURE)

The importance of high mineral fertility for successful ryegrass-based pastures was recognised early by Cockayne (1914), despite ryegrass being a better competitor than white clover when ion concentrations were low (Mouat & Walker 1959; Jackman 1965). Lambert *et* al. (1986) verified higher ryegrass content on hill country with higher fertility and rotational grazing.

Ryegrass responses to minerals are affected by environment, notably soil type and soil water content. Positive interactions in ryegrass growth between nitrogen and phophorus have been demonstrated by Luscombe *et* a/ (1981) and Mouat & Nes (1983), these correlations apparently occurring mostly where nitrification is low (Steele & Saunders 1980).

The uptake of N, K, Mg, Mn, P, Se and S by ryegrass is affected in urine patches (Joblin 1981) and funcicidal sprays interfere with these changes for N, Mg and P (Joblin & Keogh 1979). Powell (1977) drew attention to the possible role of micorrhizal fungi in ryegrass nutrition, but Parfitt *et* a/. (1982) found no response by ryegrass to mycorrhiza inoculation.

A 10% reduction in ryegrass growth was induced by Mn at 1110 mg/kg shoot DM, and uptake was higher at pH 5.5 than pH 6.5 (Smith et *al.* 1983). Ryegrass was far more tolerant of Mn than lucerne or white clover. Similarly, ryegrass is unresponsive to Cu on soils deficient enough to produce a growth response from clover (Sherrell & Rawnsley 1982), and is unresponsive to applied Bo (Sherrell 1983).

Mitchell (1953, 1954, 1955) undertook the first detailed studies of the response of perennial ryegrass to environmental conditions. Using controlled environment cabinets he demonstrated how light and temperature levels affect partitioning of growth between roots and shoots.

Ryegrass tillered faster than cocksfoot and paspalum under a wide range of conditions except heavy shading (Mitchell 1955), and tillering was greatly reduced by shading only the base of the plant (Mitchell & Coles 1955). Base shading is often important in the spring when tillering stops, as heavy herbage yields accumulate, resuming only after defoliation (Hunt & Field, 1978). Ryegrass tiller densities vary seasonally, increasing in winter and decreasing after flowering (Hunt & Field 1978), the winter build-up being accentuated by more frequent cutting (Hume & Lucas 1987).

Mitchell (1956) established that the temperature optimum for the growth of perennial ryegrass was 18-20-C and that growth at temperatures between 10 and 30°C responded to light. These optima are well below soil surface temperatures in summer, and exposed tillers without the tussock habit (seedlings for example) can be heated above air temperature (Mitchell 8 Bieleski 1964).

Also in controlled environments Hunt & Halligan (1981) and Hunt 8 Thomas (1985) studied the full range of light and temperature conditions that support ryegrass growth. Mitchell's results fitted a general pattern of growth reaching light saturation at all temperatures, with the shape of the light response curve being temperature dependent. The appearance of leaves, roots and tillers responded in the same way, and leaf appearance in part determined the potential rates of tiller and root appearance. A comprehenisve picture thus emerged of vegetative plant development and its response to current conditions. Hardacre et *al.* (1986) showed that ryegrass swards respond to CO,, although less than clover.

Brougham drew attention to interaction between ryegrass (and clover) leaf area and light interception. He described in detail the S-shaped pasture regrowth curve (Brougham 1956), and showed fundamental differences in light interception parameters between ryegrass and clover (Brougham 1958, 1960).

Seeking to optimise light interception, Brougham (1959) found that although longer regrowth periods favoured ryegrass growth, more frequent grazings (e.g. in winter) may be necessary for the best utilisation. Hard winter and lax summer grazing was recommended (Brougham 1970), although Harris 8 Brown (1971) found hard winter grazing could depress winter and the subsequent spring growth at Gore. Attempts to maintain continous high leaf area in rygrass swards led to the deterioration of the sward structure through the build-up of litter (Hunt & Brougham 1966).

Hunt (1971) related declining growth late in the ryegrass regrowth curve to increased losses from death of larger senescent leaves until death equalled growth. Chapman et al. (1984) showed that leaf death rates and longevity were unaffected by grazing management in hill country. Leaves lived longest in winter and shortest in spring and summer. Hunt (1983) noted the role of senescent leaves in N cycling, returning 10-20% of N uptake to the soil. This figure is affected by N application increasing N content of litter.

From the 1950s, ryegrass research also increased in detail to include studies of responses of organs, tissues and cells to environmentals variables (Soper & Mitchell 1956; Mitchell & Soper 1958; Forde 1966).

Physiological studies of ryegrass were extended to the biochemical level by Taylor *et* al. (1971) and Hardacre *et al. (1986).*

Evans (1964) found that although perennial ryegrass tillered faster than Italian, the latter was less affected by shading, thus perhaps enabling a greater tolerance of heavier sward yields. Greater structural material in perennial ryegrass gives it harder and more erect leaves.

Jacques with his students at Massey studied the root system of ryegrass from the mid 30s to the mid 50s. Jacques (1935) first noted glossy with new roots and darker, brown roots are various stages of ageing. Jacques (1956) described an annual pattern with some overlapping of new roots with deep roots of the previous year. This pattern determines the soil layers where absorption occurs at different times of the year.

Evans (1970, 1977) further studied the root system and effects on it of climate and management. A single defoliation caused a rapid drop in root elongation and a gradual recovery. Repeated defoliation prolonged the depression of elongation and even caused root death. Ryegrass was more severly affected than clover.

(4) RYEGRASS DISEASES

Neill 8 Hyde (1942) studied blind seed disease which results in ryegrass seed crops with reduced germination. They established the casual agent, its life cycle and conditions favourable to it. Gorman (1940) showed that crop management affected disease development, and applied N was shown to reduce blind seed disease by Hampton & Scott (1980).

The most evident diseases of the ryegrasses in New Zealand are crown and stem rusts (*Puccinia coronata* and *P. graminis*). Crown rust occurs particularly when warmth and humidity coincide. It impairs photosynthetic efficiency and renders the herbage unpalatable (Corkill, 1956). Available green leaf of Ruanui is more susceptible than of Manawa (Cruickshank 1957). Lancashire & Latch (1966, 1970) found Ruanui was more heavily infected than Ariki with up to 53% yield loss in pure swards, and weakened contribution to a mixed sward. Fertiliser N resulted in more clean growth on Ruanui, but greater infection of Ariki.

Stem rust is not usually a problem for early-flowering cultivars. However, on later-flowering material, or in an early year, it can seriously reduce seed yields through damage to photosynthetic tissue (Hampton 1986). Further, lesions occur on the leaves as for crown rust, and stem rust may be more serious in drier regions such as Canterbury. In contrast to the situation with crown rust, Nui and Ellett are more susceptible than Ruanui (Latch, pers. comm.).

Latch (1977, 1980) showed that barley yellow dwarf virus was widespread in perennial ryegrass swards more than 2 years old. Yield of infected simulated swards was over 20% lower than that of virus-free swards.

Disease of ryegrass seedlings by soil-borne fungi can be reduced, with fungicide treatment increasing seedling establishment and early productivity by up to 70% (Falloon 1980).

Litter decomposers produce toxins that can directly affect animal health and performance (Brook 1963; di Menna & Parle 1970). Facial eczema can be related to toxins produced by fungal saprophytes.

(5) PASTURE PESTS

The ryegrasses are severly attacked by most of the important pasture pests in New Zealand.

New Zealand grass grub larvae (*Costyletra zealandica*) are more severe on the roots and survival of perennial ryegrass than on Yorkshire fog (Radcliffe 1970), prairie grass cocksfoot and tall fescue (Kain et *al.* 1979). Kain & Atkinson (1977) found larvae numbers to be lower under pastures of Yorkshire fog, Poa *pratensis* and *Phalaris tuberosa* than under perennial ryegrass. Cocksfoot and tall fescue suffer production losses under severe attack, but outproduce perennial ryegrass at intermediate to high larval densities (East et *al.* 1982).

Similar but less extensive comparisons of grass species have been undertaken for porina caterpillar (Wiseana *cervinata*) (Farrell et a/. 1974), soldier fly (*Inopus rubriceps)* (Gerard & Parr 1977), black field cricket (*Telegryllus commodus*) (Blank & Olsen 1979, 1987), white fringed weevil (Graphagnathus *leucoloma*) (East 1976) and black beetle *(Heteronychus arator)* (King 1976).

Argentine stem weevil (Listronofus bonariensis) assumed prominence in the 1960s (perhaps after the widespread use of Manawa) and can destroy swards of ryegrass free of the Acremonium endophyte. Before discovery of the role of the endophyte (Prestidge et *al.* 1982), differential tolerance of cultivars had been claimed (Kain et a/. 1977; Goldson, 1979). Prestidge et al. (1985a) showed ryegrass content of new pastures surveyed in Waikato to fall from over 90% to barely 35% in 3 years. All surviving tillers harboured Acremonium and stem weevil attack of endophyte-free plants was suggested to be the major reason for ryegrass loss. Stem weevil larvae are not affected by the endophyte (Prestidge et al. 1985b).

Activity varies with district (Pottinger 1961; Barker et *al.* 1984a; Prestidge & van der Zijpp 1985). Adult stem weevil feed more readily on grass high in N, so that spring fertiliser N renders low endophyte ryegrass particularly vulnerable (Hunt & Gaynor 1982).

Various nematodes may impair ryegrass growth in pasture (e.g. Yeates & Barker 1986; Watson et *al.* 1986), but their real importance has not been established.

(6) THE **RYEGRASS** ENDOPHYTE

Endophytic fungi were first noticed in New Zealand ryegrass by Neill (1940), but it was Fletcher 8 Harvey's (1981) discovery that endophyte caused ryegrass staggers that awakened interest in them. Since then, many different grasses, including some annual ryegrasses, have been shown to be infected, each with different types of endophyte (Latch *et* al. 1988).

Of the two endophytes widespread in perennial ryegrass pastures, only Acremonium *lolii* has important effects on plants, animals and insects (Gaynor et al. 1983). In addition to causing staggers, infected grass can have subclinical effects depressing sheep liveweight gains during spring (Fletcher 1986). Infected ryegrass is also less palatable to stock

Acremonium *lolii* confers resistance to Argentine stem weevil in infected plants (Prestidge *et* al. 1982) and seedlings (Stewart 1985). Even non-viable endophyte may confer temporary seedling protection. Oviposition is reduced (Gaynor 8 Hunt 1983; Barker et al. 1984b) and larval survival is also poorer on endophyte-infected ryegrass (Barker et *al.* 1984c).

Acremonium *lolii* in tyegrass produces the neurotoxins lolitrem A and B (Gallagher et *al.* 1981) and the feeding deterrent peramine (Gaynor & Rowan 1985).

Methods were found for purging ryegrass of endophyte or infecting ryegrass with it (Harvey et *a/.* 1982; Latch 8 Christensen 1985), and for measuring host endophyte concentrations in tyegrass tissue (Musgrave & Fletcher 1986) so that effects on plants could be studied. Latch *et al.* (1985) found that under optimum growing conditions, Acremonium *lolii* in perennial ryegrass resulted in faster tillering, although negative effects on Ariki seedling growth can occur at low light levels (Keogh & Lawrence 1987). Higher ryegrass tiller densities which enhance persistence and improve productivity are associated with endophyte infection (Fletcher 1986) and may result from the lower stem weevil damage or the phytotonic effect, or both.

Sutherland 8 Hoglund (1989) found high endophtye ryegrass to suppress clover growth and density to the extent that soil N levels were lowered sufficiently to reduce subsequent crop yields.

Endophyte infection is transferred to the next generation by seed (Neill 1940). The viability of the fungus in stored seed is very dependent on conditions. Where moisture content is kept below 1 1%, and temperatures below 5°C (Rolston *et* al. 1986), endophyte viability may last 15 years (Latch 1983).

Although not eliminating it, applied N can reduce endophyte concentration in the seed, which is reflected in the subsequent plants for at least 6 months (Stewart 1986).

(7) RYEGRASS HERBAGE QUALITY

Livestock fed to appetite grow faster on a diet of legumes than on grasses, and faster on leafy Italian ryegrass than on perennial (e.g. Rae *et* a*l*. 1963). Ulyatt (1981) reported growth rates on white clover, Italian ryegrass, Ariki ryegrass and Ruanui perennial ryegrass to be in the ratio of 192:160:111:100.

The levels of protein (Johns 1955) and carbohydrate (Bailey 1964) in the diet were generally found to be satisfactory, and could not explain differences in growth rate.

Differences in liveweight are associated with differences in intake and not with digestibility. Johns et a*l*. (1963) had shown that sheep fed perennial ryegrass had greater rumen contents and lower rumen volatile fatty acid concentrations than sheep on short rotation tyegrass. Ulyatt & Macrae (1974) found that white clover passes more rapidly through the rumen, and more white clover digestion, particularly of protein, occurs in the small intestine. Animal performance on ryegrass might be better if feed moved more rapidly through the rumen. Wilson (1965) selected for low leaf tensile strength and low cellulose, and Sleper & Roughan (1984) suggested selection for rate of digestion in cellulase. Dry matter content is related to dry matter intake (John & Ulyatt 1987) but wilting does not induce a favourable effect.

By any criterion, herbage quality drops as ryegrass approaches heading and becomes stemmy. Thus digestibility declines with prolonged grazing intervals (Bell

1985), and late spring and summer management must maintain leafiness.

The mineral levels of ryegrass herbage are generally adequate if animals are fed adequately (Grace 1983), though Mg and Na are sometimes marginal. Levels vary with season and with microsite in a paddock (Butler & Johnson 1957; Reay & Marsh 1976; Crush 1983). Short rotation ryegrass has lower levels of P, Mg, K, Na, Fe, Mn and Cu per kg of dry matter than perennial. The leaves have higher mineral levels than the stem. Liming increases Ca and Mo, but decreases Mg and Mn (Edmeades et *al.* 1983).

ASSOCIATED RESEARCH

Areas of research on pastures generally, of which ryegrass has been an important component but which are not included above include: Sear's work on nitrogen cycling and fertility, pasture surveys such as those of Radcliffe, Brougham and Grant, pasture management studies, comparing rotational grazing and set-stocking, fertiliser and lime experiments, conservation and factors affecting utilisation and quality.

CONCLUSION

The themes of ryegrass research can be seen to have shifted as the intensity of work has increased. Notable periods have been the work on strains in the late 1920s, the study of temperature and light effects on growth in the 1950s, of light relations also in the 1950s, leading to interest in competitive interactions in the 1960s, and studies of tiller populations in the 1970s and 80s. The most recent major development has been the study of the Lolium endophytes.

Notable areas waiting further study are the factors affecting ryegrass failure, and means of improving ryegrass quality. In both these areas there are several hypotheses. Recent research in animal nutrition provides interesting leads, but good data are lacking on the relative importance of the elements which undermine ryegrass persistence.

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