Pasture resilience reflects differences in root and shoot responses to defoliation, and water and nitrogen deficits

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Abstract

The yield of a pasture is directly proportional to the amount of light plants intercept and allocate to different organs. When plants are carbon (C) limited, due to defoliation, they allocate more C preferentially to shoots to restore leaf area. In contrast, water and nitrogen (N) limitations lead to a greater allocation of C to roots. Changes in the root:shoot ratio therefore reflect changes in C and N partitioning and indicate their relative priority. A major factor that influences plant responses to stress is their ability to store and remobilise reserves to restore leaf area. Species with tap roots, like lucerne, have a large potential C and N storage capacity that is utilised seasonally for storage and remobilisation. This has been used to develop seasonally based grazing management rules. Similarly, recommendations to graze perennial ryegrass at the 2- or 3-leaf stage are based on the balance between maximizing growth rates and the need to replenish water-soluble carbohydrate reserves. However, perennial ryegrass has lower levels of perennial reserves than other grass species. This reduces its resilience to concurrent water deficits or N deficiency. Under these conditions maintaining the recommended 3-leaf grazing intervals and/or leaving higher post-grazing pasture masses are recommended to assist canopy recovery. Other grass species, such as cocksfoot and tall fescue, provide more resilience, particularly in response to water deficits.

Keywords: alfalfa, *Lolium perenne* L., *Medicago sativa* L., plant development, plant growth

Background

Plant communities with non-limiting water, nutrients and light maximize production. However, resource availability fluctuates for individuals within the community of plants so their ability to thrive is dependent on their ability to compete for the most limiting resource at any given time. Therefore, the collective success of sown, compared with weed species, reflects the ability of individual plants to capture sufficient carbon (C) and nitrogen (N) to grow and maintain perennial organs. That success in resources capture within a grazed sward determines pasture resilience and persistence. The frequency and intensity of grazing affect the total amount of C captured (Chapman et al. 2014) through photosynthesis and consequently the amount available to allocate to roots and shoots. Grazing removes the shoot green leaf area as a feed source. Post-grazing recovery requires emergence of new leaves, which is a development process, to restart the growth (C capture) process. Each new leaf is initiated on the growing point of the plant. The size of a newly emerging leaf is a consequence of the C, N and water available to support cell division and expansion during its initiation. These new leaves are initially a sink for assimilate and expand aided by the importation of C and N reserves from the residual leaf sheath (pseudostem) and roots. Therefore, any biotic (grazing), abiotic (environmental), or edaphic (soil) factor that reduces the total amount of residual leaf area and C and N reserves affects initial pasture recovery rate and pasture resilience over time.

The plant species present also determines how quickly a pasture recovers and survives grazing. Carbohydrates in grass species which have fine, fibrous roots are turned over rapidly through a season and after a grazing event. Initial regrowth of the new leaf includes remobilization of C and N reserves from the leaf sheath or pseudostem (Briske & Richards 1995). In contrast, species with tap roots, such as red clover (*Trifolium pratense* L.) and lucerne (*Medicago sativa* L.), invest C and N preferentially during establishment in root and crown structural components (Thomas 2003) and have large stores of root reserves to remobilise after defoliation (Yang 2020). The removal of green leaf area stimulates the remobilization of reserves from these structures to initiate new leaves. As these leaves develop and grow they photosynthesize and become net exporters of C and N to support the young leaves higher in the canopy (Hay & Porter 2006). The duration of remobilisation to support new leaf, tiller or branch growth differs amongst species and cultivars and this also has consequences for their ability to survive defoliation and other stresses.

At some point in each regrowth cycle plants must replenish C and N reserves by partitioning C and N to storage organs. Without this, the reserves decline and eventually the plant dies. In practice, this requirement is considered in grazing management recommendations. For grasses, defoliation may be linked with the

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appearance of the third (Chapman et al. 2014) or fourth green leaf (Hendriks et al. 2016). The aim is to minimise the lag phase of recovery and ensure the canopy of green leaves has recovered to maximise the period of linear growth before the ceiling yield (Brougham 1955, 1957).

The interval between grazing events must also provide sufficient recovery time for C and N reserves to be partitioned back to storage organs. This interval is influenced by the post-grazing pasture mass (PGPM) which provides the residual green leaf area for initial new leaf growth, and abiotic conditions (Chapman et al. 2014). For specialist legume-based pastures strict grazing rules are frequently advised. For plantain (*Plantago lanceolata* L.) and red clover, grazing recommendations are based on a higher entry and exit cover than are normally used in grass-based pastures (Cranston et al. 2015).

Best management practices have been developed for many pasture systems and species. These rules must also be changed in sub-optimal conditions caused by biotic or abiotic stress. Under water deficits leaf extension is reduced so that the time to canopy closure is increased. The consequence is that less of the available light is intercepted which reduces the daily photosynthate production to below the environmental potential. As water deficits increase, photosynthesis itself declines and stomata close and evaporative cooling ceases. Under dry soil conditions, plant and soil temperatures rise (Watson et al. 1995) and so do plant respiration rates, which depletes plant reserves and leads to plant death. Thus, refining practices in response to changing biotic and abiotic stresses is the key to pasture persistence and resilience.

Approach

This paper emphasises plant growth (C capture) and development (organ initiation) including changes in the root:shoot ratio as the indicators of plant responses to management and environmental conditions. The responses of different grasses and tap-rooted legumes are used to illustrate principles that can be applied to different species.

In most cases lucerne and perennial ryegrass (*Lolium perenne* L.) are used as model plants to represent tap- versus fibrous-rooted species, although examples of species differences are also highlighted. The paper outlines the general pattern of dry matter (DM) accumulation and partitioning of each species under non-limiting conditions and then explains how biotic and abiotic factors impact on plant growth. The aim is to provide the physiological basis for understanding how plants respond to defoliation, and water and N deficits. These responses are used to explain principles of grazing management that balance animal production and pasture resilience.

Pasture Production

The total amount of assimilate (sugars) produced by a canopy of leaves determines the amount available for partitioning to roots and shoots that ultimately dictates pasture production and plant resilience. In its simplest form the herbage yield (Y) of pastures is a function of the amount of incident light intercepted by a canopy of green leaves (energy supply; I/I_o) and the efficiency with which that light is converted to DM (RUE; Equation 1). The canopy of leaves is quantified by the product of the size and density of grass tillers or lucerne stems as the dimensionless green area index (GAI). This is the ratio of green leaf area, from one side of leaf lamina, to the ground area. Values of GAI are difficult to measure in low growing, grass-based pastures but range from ~1.0 immediately after a hard sheep grazing to 3.5 at canopy closure, or GAI_{crit}, when 95% light interception occurs. For the more erect lucerne, virtually all green leaf material can be removed during defoliation when the post-grazing GAI would be closer to 0 and then recover to a GAI_{crit} ~3.8. The recovery of leaf area requires the appearance and expansion of new leaves. Leaf appearance is a conservative development process (Chapman et al. 2014), with the interval between new leaves (phyllochron) quantified by thermal time and modified by photoperiod in some species (Brown et al. 2005). The rate of expansion and final size of these leaves are growth processes, dependent on the availability of C, N and water. Leaf expansion (growth) is more affected than leaf appearance by overgrazing (Chapman et al. 2014), sub-optimal temperatures, and supplies of water and nutrients.

$$Y = I/I_o \times RUE \qquad [\textit{Equation 1}]$$

Where I/I_o is the fraction of incoming total incident, or photosynthetically active radiation, intercepted by the canopy (MJ/m^2), which represents energy supply, and RUE is radiation use efficiency (g DM/MJ/m^2) which represents conversion efficiency.

The recovery of a pasture after grazing follows a sigmodal or S-shaped pattern (Brougham 1955, 1957). The initial lag phase represents the time required to recover leaf area to start accumulating DM in the new and emerging leaves. Minimising this phase is important because light is instantaneous. If light is not intercepted by green leaves then it is lost from the system and represents a loss of potential yield. Thus, rapid recovery of the GAI is vital to maximise yield (Equation 1). This will be affected by the intensity of grazing and the consequent ability of plants to remobilize C and N reserves. Biomass accumulation is most rapid during the linear phase until ceiling yield is reached. The ceiling yield occurs when the daily rate of photosynthesis is equal to the maintenance requirement of the standing biomass. At this point the rate

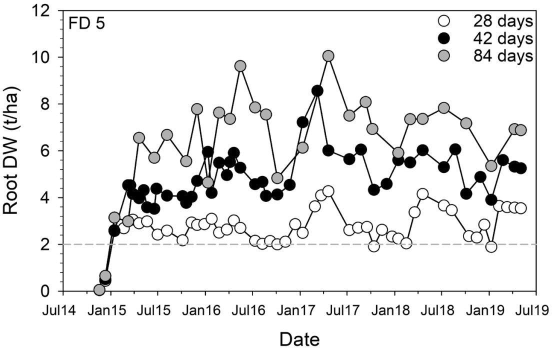

Figure 1 Change in perennial (root + crown) biomass (0-0.3 m) over time of irrigated 'Grasslands Kaituna' lucerne (fall dormancy (FD) rating = 5) subjected to regrowth cycles of 28, 42 (commercially recommended) or 84 days during active growth for five growth seasons (2014/15 to 2018/19) at Lincoln University, Canterbury, New Zealand (data source: Ta 2018; Yang 2020). The horizontal dashed line represents structural perennial biomass which cannot be remobilised.

of DM production equals the rate of DM loss through respiration and senescence (Bircham & Hodgson 1983). In practice, managers strive to avoid this phase preferring to defoliate at the end of the linear phase. The consequences of allowing standing herbage to accumulate further can be interpreted from conserved pastures. Grass-based hay and silage making usually occurs in spring when total herbage yields are increased by seed head appearance. This results in a loss of quality as herbage mass increases and is consistent across temperate grass species (Greenwood et al. 1990; Lemaire & Maynard 1997; Mills et al. 2009) and lucerne cultivars (Ta et al. 2020). The decline in quality is due to an increase in the quantity of structural tissue (fibre) and the accumulation of dead and senescing material as shaded lower leaves remobilize N to the younger leaves at the top of the canopy. The taller herbage also requires greater structure to support the canopy and stem which increases the unpalatable fibre content.

Impact of defoliation on lucerne root reserves

At the forage crop level, the impact of different durations between defoliation events has recently been examined for lucerne. Over 5 years at Lincoln University the above- and below-ground (root and crown reserves) biomass accumulation for lucerne crops defoliated at either 28-, 42- or 84-day (d) intervals was measured. The longest regrowth duration had 2 or 3 t DM/ha more ($P<0.01$) crown and root biomass than those defoliated after 42 days. This enabled 4-6 t DM/ha to be remobilised from these crops during the spring period. The lucerne defoliated at 42-d intervals, in turn, had higher crown and root reserves than lucerne defoliated at 28-d intervals (Figure 1). The pattern of increased partitioning to roots in autumn and remobilisation to shoots in spring was also evident, which supports previous work that showed partitioning in lucerne to and from perennial organs is strongly affected by photoperiod (Moot et al. 2003). In spring, remobilisation of root and crown reserves results in greater shoot growth rates than in autumn at the same corresponding temperature. The seasonal pattern of accumulation and depletion of crown plus root reserves is also apparent in Figure 1. Sim et al. (2015) suggested that at least 5 t DM/ha of crown and root reserves are required to consider a lucerne crop established, while Yang (2020) determined that ~2 t DM/ha of this was structural and could not be remobilised. This was consistent with Teixeira et al. (2007) who showed that continuous 28-d defoliation during active growth reduced perennial reserves to below a critical 3 t DM/ha, allowing weed ingress, and resulted in stand collapse. The mechanism of stand collapse was the loss of canopy closure due to a reduction in the individual stem weight and leaf size, rather than any acceleration in the rate of self-thinning of plants commonly found in lucerne stands.

Investigations of lucerne crown plus root reserves (C and N) have led to changes in grazing management recommendations. Emphasis is now on recharging these reserves in autumn to maximise spring regrowth for animal intake (Moot et al. 2003). In practice this fits the dryland sheep and beef industry where a high number of animals are produced in spring with a need for rapid animal growth rates to allow destocking at, or before, the summer dry arrives (Avery et al. 2008; Moot et al. 2019). This grazing approach has been successful in Argentina (Berone et al. 2020) compared with previous recommendations to allow 10% flowering before defoliation (McLeod 1978; Kirsopp 2001). Recommendations to allow 10% flowering historically came from management guidelines developed in the United States where "alfalfa" is predominantly a conserved feed in a cut and carry system. They also reflect the drastic defoliation that routinely occurs for grazed and cut lucerne crops where all leaf material is removed. Thus, there is a period of regrowth immediately after defoliation that is solely dependent on remobilisation of C and N reserves to re-establish the canopy. This led to the recognition of a period of depletion and recovery in each successive regrowth period for lucerne crops and a universal recommendation for rotational grazing. Yang (2020) quantified this period of remobilisation as 350 °Cd growing degree days post-grazing in spring for standard cultivars (FD5) used in New Zealand. Yang (2020) also showed that, provided the grazing interval was ~350 °Cd and plants were given an extended (500 °Cd) autumn rest to recharge reserves depleted in spring, root and shoot reserves can recover to enhance the resilience of the crop in future years.

Lucerne grazing management

Further refinement of the grazing recommendations for different classes of livestock is based on grazing height of the lucerne rather than any pre-set grazing interval or plant development stage (Moot et al. 2016). A feature of these recommendations is the trade-off between crop yield and quality. Brown & Moot (2004) suggested that in any given lucerne crop there is ~2.5 t DM/ha of high quality leafy herbage. Thus, growing crops to higher biomass results in a greater proportion of stem which proportionately reduces the herbage quality. Ta et al. (2020) quantified this trade-off and supported the conclusion to graze when 3 t DM/ha is present to balance quality, quantity and persistence, provided the autumn rest period is adhered to. Indeed Sim & Moot (2019) suggested that lucerne could be set-stocked over lambing in spring provided a canopy of leaves was maintained to reduce weed ingress and crops were rested to allow root recharge in autumn. These recommendations have been implemented successfully on-farm (Avery et al. 2008; Anderson et al. 2014; Moot et al. 2019) and provide the basis for management recommendations sent to ~1300 farmers weekly on a Beef + Lamb New Zealand text alert service (https://beeflambnz.com/user/newsletter-signup).

The principles utilised in developing the lucerne grazing system are equally valid for investigating best management practices for other species. Considerable research effort has gone into developing detailed understanding of perennial ryegrass growth in response to defoliation and other stresses. Despite this there is a perception that perennial ryegrass-based pastures fail to persist. It is prudent to summarise the growth and development of grass plants compared with the large rooted lucerne to understand the key concepts and consequences of mismanagement.

Growth pattern of perennial grass plants

One comprehensive example of how a grass plant grows is a multimedia package (Ashley et al. 1997), recently placed online (https://www.nottingham.ac.uk/ toolkits/play.php?template_id=11419), and used as the source for the information summarised here. The morphology of grass plants is modified by grazing intensity as an adaptive strategy that adds resilience to individual plants and the canopy of leaves. Typically, close-grazed sheep pastures have more but smaller tillers than those grazed by cattle. The individual grass plants that make up the sward are comprised of tillers, with 300 plants and 5000-10000 individual tillers per square metre. Tillers form in the axils of leaves at ground level in vegetative plants. Individual leaves are short-lived and surrounded by decaying leaf sheaths which form the pseudostem that contributes to the initial recovery after grazing (Chapman et al. 2014). Once three or four leaves are present on a tiller, old leaves senesce and new leaves continue to form, so the number of living leaves remains constant. These living leaves contribute to the 'phytomer', which is the basic unit of a grass plant. New phytomers are continually formed at the base of the pseudostem, from the growing point.

The arrangement of phytomers determines the grass growth form and its ability to withstand grazing. The ryegrass phytomers are arranged like a stack of dinner plates at the base of the pseudostem. Therefore, its vegetative tillers are short and located near ground level. In contrast, kikuyu (*Pennisetum clandestinum* Horst.) has greater internode elongation, and leaves remain alive for longer. This results in its creeping growth form with leaves spaced along an extended stem. Both growth forms provide grazing resistance and prevent damage to growing points. The extended stem of kikuyu and similar species such as browntop (*Agrostis capillaris* L.) confer greater grazing tolerance than for perennial ryegrass (Briske 1996).

In a sward with a constant tiller population, each parent tiller produces only one daughter tiller. The number of tiller buds which develop into daughter tillers is just enough to replace the tillers which die. However, this is about 10-20% of tiller buds formed. The dormant buds provide opportunity for a rapid regrowth or a "gap-filling" response when nutrient and light quality (red to far red ratio) conditions are favourable (Hay & Porter 2006). This ability to alter the tillering response is the morphological mechanism that enables them to recover from defoliation, water deficits or N deficiency.

Scientists have counted tiller numbers, assuming higher numbers indicates a more productive pasture. This is sometimes, but not always, true. In ryegrass-based dairy pastures there are typically 4000-8000 tillers/m^2, while in sheep pastures there may be 8000-20000 tillers/m^2. The lower tiller density in the grazed dairy pasture occurs because cows usually graze pasture at a greater average herbage mass, so fewer daughter tillers are initiated and individual tillers are larger. This trade-off between tiller size and tiller density represents size/density compensation.

One way to examine the tiller size/density compensation is to plot tiller size and tiller density, both on a log scale, and draw the sloping compensation line. This line has a theoretical slope of -3/2. A decrease in defoliation height causes swards to drop below the compensation line (Matthew et al. 1995, 1996). In essence grass swards can adapt readily to different grazing heights through tiller size/density compensation.

Roots

As shown for lucerne (Figure 1), roots are a major storage organ for C and N and impacted by defoliation and other stresses. However, roots are difficult to study in the field. The Grassview resource (Ashley et al. 1997) documents only one study that measured root development of ryegrass on a nodal basis (Matthew & Kemball 1997). A ^{14}C tracer estimated the amount of current photosynthate reaching each root. The length of the main root axis did not exceed 0.4 m, but total length with branches exceeded 2.0 m, so each tiller had more than 10 m of root length. Thus, under a pasture of 5000 tillers/m^2 there are ~70 km root/m^2.

In the same study, younger roots received more photosynthate than older roots. Photosynthate (C) supplied to young roots is concentrated in root tips where root elongation is occurring. Reduced supply to older roots, such as due to high rates of defoliation, stops root elongation, and can eventually cause death. Root development is also a coordinated process between successive phytomers in the same way as for leaves. Therefore the cycling of roots is similar to the cycling of leaves. Note though that there are up to 10 nodes with roots attached, but only three or four nodes with emerged leaves, so the lifespan of a root and the turnover intervals for roots are longer than for leaves.

These development processes for leaves and roots are the building blocks for recovery of pastures after grazing. The impact of grazing can be viewed through its impact on the ability of plants to recover leaf area through the growth of tillers, phytomers and roots.

Impact of defoliation on grass swards

Much has been written about pasture responses to grazing. Two classic references summarise how leaf elongation at the tiller level is reflected at the paddock level. First, a 1950's study (Brougham 1955) showed how herbage mass changes with time after grazing, which accentuated the sigmoid growth curve with lag, linear and ceiling phases of growth. In the 1980s Bircham & Hodgson (1983) highlighted the balance between leaf elongation and death at different levels of herbage mass under continuous stocking management with sheep. Specifically, in short swards (sward surface height of 1-2 cm or herbage mass of 500-700 kg DM/ha), net production is low due to reduced leaf area formation. In medium-length swards (3-5 cm or 1100-1500 kg DM/ha), net production was relatively constant, and near the maximum, over a wide range of sward heights and in long swards (7-8 cm or 1700-2000 kg DM/ha), net production was decreased due to high leaf death rate. This highlights how the intensity of grazing affects pasture production.

One of the most extreme examples of constant defoliation of grasses occurs in turfgrass management. Here grasses are managed for sport and recreation at low (0.5-5.0 cm) cutting heights through frequent mowing (Beard 1972). In turfgrass systems, such as a golf course green, turfgrasses are mown at <0.5 cm every 1 or 2 days. This results in reduced plant size, and increased tiller number but reduced root mass (Madison 1962). In a study of browntop, creeping red fescue (*Festuca rubra* L.), and Kentucky bluegrass (*Poa pratensis* L.), lower mowing heights resulted in smaller stems, finer leaves, shorter roots, and reduced storage organs such as rhizomes. Consequently the turf had a greater need for N fertilisation than one mown less frequently (Harrison 1931). Smaller plants have reduced root length and therefore less capacity to acquire nutrients which in turn lowers their stress tolerance (Sullivan et al. 2000) and limits their ability to survive stressful events. Total photosynthesis per unit of ground is reduced due to the reduction in leaf area which decreases the amount of light intercepted (Equation 1). The consequence is reduced carbohydrate reserves because they are constantly remobilised to regrow leaves, at the expense of the roots, in a C-limited system (Liu & Huang 2003; Howieson & Christians 2008). For example, creeping bentgrass (*Agrostis stolonifera* L.) swards that were maintained at 25% lower heights than control swards had greater root death and less new root generation, particularly during warmer summer months when water deficits are more common (Liu & Huang 2002). Many pasture and turf grasses can survive continuous grazing or mowing when resources such as water and N are abundant. However, they will decline rapidly when conditions such as reduced soil water content or heat stress occur in summer.

At the extreme, management of turfgrass is analogous to continuous overgrazing under a set-stocked regime, most commonly used in hill country. A lack of C leads to greater allocation of assimilate to tillers/leaves at the expense of roots and other storage organs (Briske & Richards 1995) which decreases pasture resilience (Cullen et al. 2006a). There is a similar need to constantly supply non-limiting water and nutrients to maintain sward resilience, which is impossible in most hill country areas. Leaf removal results in C-deficient plants that produce smaller and smaller leaves and consequently reduced light interception. Plants also become N deficient as root growth is curtailed and become vulnerable to water deficits. The alleviation of stress, for example by the application of N, can result in high herbage yield responses (Fasi et al. 2008; Lambert et al. 2012), due to greater light interception through increased leaf extension and increased photosynthetic rates (Equation 1). Equally, a period of deferred grazing is recommended to increase pasture resilience in traditionally set-stocked areas (Tozer et al. 2014), which will allow restoration of C reserves, increased leaf area and greater root growth.

For rotational grazing more precise grazing rules have been developed based on the appearance of new leaves. In a cutting experiment Fulkerson & Slack (1995) showed that the water-soluble carbohydrate content of pseudostems was reduced to 2.5% when cut at the 1-leaf stage compared with 17.5% when cut at the 3-leaf stage. They concluded that perennial ryegrass should be defoliated at the 3-leaf stage to maximise growth, replenish reserves and ensure regrowth in the following cycles. Subsequent recommendations have set a minimum grazing level for perennial ryegrass at the 2-leaf stage (Fulkerson & Donaghy 2001). The implication is that once two leaves have emerged fully there is sufficient restoration of C reserves to support post-grazing recovery. In non-limiting conditions the appearance of the second leaf will be driven by the accumulation of temperature. However, under mild soil water deficits leaf appearance and respiration rates will accelerate due to increased canopy temperatures. There are few data available on the implication of this for these grazing rules but it would appear prudent to delay grazing until closer to the 3-leaf stage under water deficits. In practice it is possible that the opposite management occurs, as feed shortages develop due to slower recovery from grazing, which reduces pasture resilience.

Comparative analyses of grass species show different responses to defoliation. Overall, perennial ryegrass is the most sensitive, and least resilient, to defoliation because it partitions a higher proportion of assimilates to leaf growth and has more rapid leaf turn-over compared with more resilient cocksfoot (*Dactylis glomerata* L.), which has a higher sheath to stem ratio, and tall fescue (*Schedonorus phoenix* (Scop.) Haheb.) (Cullen et al. 2006b).

Grass responses to water deficits, nitrogen deficiencies and defoliation

Plants begin to show sign of dehydration (water deficit) when water supply is below evaporative demand. This reduces plant growth, hastens phenological development, and decreases plant survival. When the availability of water is limited, the first process affected is cell expansion. This is due to the reduction of turgor pressure in the leaf cells. Under mild water deficits, leaves continue to develop at the same rate per unit of thermal time, so the phyllochron is unaffected. However, the expansion of leaves is slower and the canopy takes longer to reach critical GAI. Thus, there is less C from the photosynthetic C reactions allocated to shoots and roots. Plants take up both water and nutrients through their roots. Under water deficits, lucerne (Luo et al. 2020) and grass (Wedderburn et al. 2010) plants allocate a greater proportion of the available C to roots at the expense of shoots, which results in a greater root:shoot ratio. A similar response occurs under N deficiency for grasses, but this is initially less obvious for legumes due to N fixation. Nitrogen deficiency may not always be detected in a herbage test, because many plants adjust their leaf size to maintain a leaf N content of about 3%, to maximize photosynthesis (Peri et al. 2002a). In practice, N deficiency is suggested by taller and greener herbage in urine patches after grazing. This added growth response to urine N can remain for several months (Peri et al. 2002b).

In addition to reduced leaf area, the water or N deficiency also affects photosynthesis (Peri et al. 2002a). This occurs directly through reductions in chlorophyll content and lower metabolic rates, and the closure of stomata because of lower turgor pressure. Under water deficits, the dual function of stomata poses a significant risk for plants. The balance of water loss against CO_2 uptake is heavily skewed towards water. For every 2.0 g CO_2 captured, most plants, including perennial ryegrass and tall fescue, lose about 1 L H_2O! When plants close their stomata to restrict water loss, it decreases both photosynthesis and transpiration. With closed stomata, the uptake of CO_2 for the photosynthetic C reactions and of soil water, to replace that lost by transpiration, are reduced severely. In extreme and prolonged cases of water deficits, leaves die (senesce). The water shortage in turn results in nutrient deficiency, as water is also the carrier for nutrients, particularly nitrate. Furthermore, the reduced transpiration rate exposes the plant to increasing heat stress due to reduced evaporative cooling. The weakened plant is more vulnerable to treading damage from livestock and attacks from pests and diseases.

A pasture system weakened already by water deficits or N deficiency can be brought rapidly to a tipping point by grazing pressure. Frequent defoliation from grazing animals can be managed in a balanced C/N/water system for the ongoing regrowth of pasture grasses. In a water-limited system, however, this balance is affected severely. Consequently, a ‘normal’ grazing regime can easily, and unintentionally, tip towards overgrazing under water deficits. If unchecked this can damage pasture systems severely. If the stocking rate is not reduced or rotation interval lengthened, there is simply insufficient feed for the same number of livestock. Unaltered, stock management under water limitation will result in a chain reaction of additive or multiplicative effects of water stress, nutrient deficiency, heat, pests, diseases and grazing pressure (Busso et al. 1989; Peri et al. 2002a; Tozer et al. 2017; Ruckert et al. 2018).

For example, water deficits put extra pressure on plant symptoms from intense defoliation (Denton et al. 2018). A study in tussock grasses (Busso & Richards 1995) showed that water deficits add to the reduction of plant growth under defoliation pressure, as discussed above for turfgrasses. The resulting smaller plants have even shorter roots and increased risk of pasture failure due to less uptake of soil water, N and other nutrients. This further depletes the root C reserves that are needed to remobilise C to the above-ground regrowth phase post-grazing. The consequence is a lengthened period of water deficits and recovery phase and decreased pasture resilience compounded by overgrazing.

Organ and species differences

There are differences in organ development depending on the nature of the limitation. When N and water are limited, grasses commonly increase their root:shoot ratio by investing a relatively higher proportion of C into below-ground growth. This decreases the drain from above-ground plant parts on the limited N and water resources. The resulting reductions in leaf extension reduce light interception and the efficiency of converting this light into shoot biomass (Belanger & Gastal 2000). This is the opposite effect of frequent defoliation, which actually decreases the root:shoot ratio by increasing the relative allocation of C into leaf formation to regain some of the C lost from defoliation.

Perennial ryegrass is particularly vulnerable in this regard when compared with other grasses. Compared with tall fescue, it has a smaller, shallower root system (Cougnon et al. 2014, 2017) and lower pseudostem reserves to store C for remobilisation post-grazing or under water stress. Relative to perennial ryegrass, tall fescue invests more C into its roots (Cougnon et al. 2017), thus increasing access to water and nutrients under water deficits, and C remobilisation to leaves post-grazing. Higher above-ground yield of tall fescue than perennial ryegrass under dry spells has been linked to the higher root biomass of tall fescue in deeper soil layers (Cougnon et al. 2014). A direct comparison of these two species found that tall fescue operates as a 'water spender' by attracting more water into its cells with its deeper root system (Butler 2008). In contrast, perennial ryegrass follows a 'water saver' strategy by conserving internal water use through stomatal closure. Whilst this increases the water use efficiency of perennial ryegrass, it means perennial ryegrass 'shuts up shop' and waits for the water deficits to disappear. The more open stomata in tall fescue maintain a level of photosynthesis and productivity under water limitation.

Management strategies

Under stress, the only reactive management response to prevent the downward spiral of reducing pasture quantity and quality in perennial ryegrass is to increase the supply of water from irrigation plus N fertiliser. Increasingly the use of such inputs is limited, questioned environmentally and/or cost-prohibitive, or impractical. Furthermore, in the context of climate change and higher frequency and severity of droughts (Salinger 2003), recovery after drought is now considered as important as the resistance of plants during a drought (Guo et al. 2020). There is a need to allow pasture recovery during periods of water limitation. A proactive approach to increase drought recovery requires more and earlier supplemental stock feed. Management during water deficits requires longer intervals when rotational grazing, reduced stocking rates and leaving higher post-grazing pasture residuals to provide reserves for recovery. Compared with other grass species, perennial ryegrass is particularly sensitive to defoliation (Cullen et al. 2006a) and such management approaches must allow perennial ryegrass to reach a more mature developmental stage (ideally three fully formed leaves per tiller) before grazing. Consequently, the species will be able to translocate more C into roots and pseudostems, thus increasing its resilience under grazing and under water deficits.

Conclusions/Practical implications/Relevance

Nobody deliberately mismanages their pastures. However, at times they may be grazed under sub-optimal conditions. The implications of doing so are clear. When plants are C-limited after defoliation they initially use root and pseudostem reserves to recover their leaf canopy. If defoliation occurs again before reserves have been fully replenished the plants will prioritise shoot growth over roots. This reduces their root:shoot ratio and increases their susceptibility to any additional water or N deficiency. When water or N limitations occur, plants favour root growth over shoot growth. However, this limits C availability so too frequent or intensive defoliation will reduce pasture resilience. Perennial ryegrass is particularly sensitive to multiple stresses due to a lack of perennial storage organs. When under stress, rotations need to be lengthened and PGPM increased to reduce the risk of pasture failure. It is imperative that farmers remain well-attuned to the weather, including to long-term predictions, and manage their pastures accordingly by growing tap-rooted species, using more supplementary feed or destocking earlier to avoid long-term pasture damage.

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