

Review

Using Ecophysiology to Improve Farm Efficiency: Application in Temperate Dairy Grazing Systems

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Abstract: Information on the physiological ecology of grass-dominant pastures has made a substantial contribution to the development of practices that optimise the amount of feed harvested by grazing animals in temperate livestock systems. However, the contribution of ecophysiology is often under-stated, and the need for further research in this field is sometimes questioned. The challenge for ecophysiologicalists, therefore, is to demonstrate how ecophysiological knowledge can help solve significant problems looming for grassland farming in temperate regions while also removing constraints to improved productivity from grazed pastures. To do this, ecophysiological research needs to align more closely with related disciplines, particularly genetics/genomics, agronomy, and farming systems, including systems modelling. This review considers how ecophysiological information has contributed to the development of grazing management practices in the New Zealand dairy industry, an industry that is generally regarded as a world leader in the efficiency with which pasture is grown and utilised for animal production. Even so, there are clear opportunities for further gains in pasture utilisation through the refinement of grazing management practices and the harnessing of those practices to improved pasture plant cultivars with phenotypes that facilitate greater grazing efficiency. Meanwhile, sub-optimal persistence of new pastures continues to constrain productivity in some environments. The underlying plant and population processes associated with this have not been clearly defined. Ecophysiological information, placed in the context of trait identification, grounded in well-designed agronomic studies and linked to plant improvements programmes, is required to address this.

Keywords: temperate pastures; dairy grazing management; pasture regrowth; herbage utilisation; farm systems

1. Introduction

The overview of the contribution of research into the physiological ecology of forage plants presented by Da Silva *et al.* [1] illustrates the critical role played by this scientific discipline in quantifying the dynamics of leaf area expansion, light capture, and sward structural and compositional changes (including fluxes of plant organic reserves) as they affect herbage accumulation in grass-dominant pastures. This information has been instrumental in developing sward management practices that maximise the intake potential of grazing animals while also sustaining high rates of net herbage accumulation. Hodgson [2] weaved the underlying science of plant and pasture growth processes into a clear account of the grazing management principles and practices that optimise the sustainable yield of herbage under different grazing methods operating in a range of environments. The science, principles and practices were further developed in Lemaire *et al.* [3].

Despite the impressive body of knowledge summarised in these two volumes and this special issue, the contribution of ecophysiology to grassland development around the world is often under-stated and the value of further ecophysiological research has sometimes been questioned.

For example, Bryant [4], in summarising optimum feed management practices for New Zealand dairy farms, concluded that over and above the implementation of current grazing recommendations, the effect of grazing management on production was small, and proposed this “... must surely signal the end of a long era in grazing management research...”. This is a bold statement, considering that maintenance of the global competitive advantage of the New Zealand dairy industry rests heavily on achieving continued improvements in the amount of feed harvested from grazed, perennial ryegrass-dominant pasture. Recent analyses indicate that New Zealand dairy farmers have lost their previous position as the lowest-cost milk producers in the world [5] and, seemingly, also lost their focus on achieving good control of pasture growth and utilisation [6]. These trends suggest that a resurgence in “grazing management research” is required: or, at least, that questions are asked about how well the ecophysiological knowledge already available is being used to reinforce management advice to dairy farmers (e.g., [7]).

The New Zealand dairy industry is built upon the combined natural elements of fertile soils, high rainfall (usually evenly distributed throughout the year), and a temperate maritime climate which allows large amounts of pasture to be grown to feed high-producing animals. It is internationally recognised as a model for how a globally competitive industry can be developed from a sustainable natural resource base without the use of price subsidies or other protectionist market policies. At the farm level, there is a close positive relationship between the amount of pasture consumed and operating profit per hectare [8], as there is in other countries with largely pasture-based dairy industries [9]. Continued gains in the amount of pasture utilised are essential for future growth of the industry at both the global and the farm levels.

The aim of this review is to use the New Zealand dairy industry as a case study to: illustrate the important contribution of ecophysiological knowledge to the development of efficient grazing management practices; show how those practices are implemented (or, as seen in some surveys, not implemented) on dairy farms; identify where existing and new ecophysiological information can be used to help improve pasture performance further; and consider how the discipline of ecophysiology needs to link to other disciplines to increase the rate of gain in pasture productivity being achieved on-farm.

2. Critical Ecophysiological Principles and Their Translation to Grazing Management Practice

The starting point for designing efficient grazing management systems is the pasture regrowth curve. Regrowth is a result of each grass tiller producing new leaves to replace leaves that were removed by grazing, thus steadily increasing the pasture mass produced over time. The typical regrowth interval in dairy grazing systems is between 20 and 60 days, varying depending on temperature, radiation intensity, and water and nutrient availability. The critical ecophysiological processes supporting the accumulation of mass have been well documented in the research reviewed in this special issue [1,10,11]. They include: the emergence and expansion of new leaves from the tiller apical meristem to replace lamina area and increase light interception and carbon (C) assimilation; the mobilisation of some stored C and nitrogen (N) to support new leaf production and Rubisco synthesis, with subsequent replenishment of those stores once the energy and N status of the whole plant recovers; changes in the relative allocation of available C between the shoot and root systems, initially to promote new leaf growth, and subsequently to resume root growth so that the capacity to assimilate nutrients and water remains in balance with the increase in C assimilation capacity of the canopy; tiller initiation and emergence and consequent effects on sward tiller density; changes in leaf morphology including the specific and absolute area of the new leaves produced as the plant responds to its changing energy status; and the turnover of older leaf material entering senescence including re-translocation of some constituents of old leaves, especially N, to support new growth.

The underlying drivers are light interception, whole-plant energy status, and the maintenance of homeostatic growth such that the balance between root and shoot (including reproductive development) maximises the long-term ability of grass plants to compete for light and other resources

and so sustain their presence within the grassland community [12]. The high degree of spatial and temporal variation in weather conditions (influencing temperature, rainfall, and total radiation receipt), nutrient distribution (including the effects of excreta return) and defoliation (which is spatially variable irrespective of whether swards are continuously or intermittently grazed, just at different scales [13]), combined with the diversity of species-specific traits governing resource capture and use found in mixed swards, makes for a highly complex system which farmers must manage. Furthermore, efficient livestock farming requires that as much herbage as possible is harvested to feed animals. But this very process removes the leaf area required for plants to sustain growth and sets up a fundamental conflict between the needs of the pasture and the needs of the animal [14]. It also sets in train repeated cycles of leaf removal and replacement, the outcome of which can be measured in terms of, for example, the total amount of herbage harvested per unit area per year, or (of more direct importance to farm profitability) the amount of animal product (milk, or meat) derived from grazed pasture per year. The degree to which these repeated cycles are managed to achieve a sustainable balance between herbage harvest rates and herbage growth rates becomes the pivot point upon which farm business success depends.

The complexity of the processes described above is daunting for scientists. As the reviews published in this special edition attest, despite decades of research into the critical ecophysiological processes, our knowledge of the interactions is far from complete. The challenge is much more daunting for farmers. A key goal for scientists working in the field of grassland ecophysiology must, therefore, be to make the “complex seem simple”. To achieve this, ecophysiological principles must be translated into easily implemented practices and decision rules (with accompanying management information resources) for farmers and their advisers. Grassland farming efficiency in the UK, New Zealand, Australia and other countries has benefitted enormously from work of this nature [15]. Examples include: development of sward height targets in the UK [2,16]; grazing rotation guidelines in New Zealand and Australia [15,17]; use of the leaf stage indicator for perennial ryegrass [18], and the compilation of comprehensive grazing decision rules [19]. Most of these apply to temperate zones, but the adaptation of the same ecophysiological principles to C_4 species is making great strides towards improving the efficiency of tropical grassland farming [1].

Even in the temperate grassland world, further efficiency gains are well within reach for farmers if new ecophysiological information can be gathered, and existing ecophysiological knowledge is re-visited, to identify how improvements in pasture harvest rates can be achieved. The clearest opportunity is to capture more of the potential for herbage accumulation available from the pasture regrowth curve in intermittent (rotational) defoliation systems. The following sections relate the ecophysiological processes of light capture, herbage accumulation, and tissue turnover in grass-based pastures during regrowth to current grazing management recommendations in the New Zealand dairy industry. They draw on evidence from on-farm studies to illustrate how opportunities for improved biological efficiency, and greater profitability, are being foregone in this industry which is often considered the benchmark against which other pasture-based livestock industries should measure their potential for improvement.

3. Managing the Pasture Regrowth Curve

3.1. *The Ecophysiological Basis of Current Grazing Management Recommendations for New Zealand Dairy Farms*

Pasture yield was first related to light interception in the 1950s. Brougham [20,21] showed that, when the pasture canopy intercepts about 95% of the available light, the rate of accumulation of pasture mass declines to quickly reach a ceiling yield that varies according to seasonal differences in light intensity and the leaf area index (LAI) that can be sustained. In the 1970s and 1980s, the flow of mass through plants and the canopy as pastures regrow up to ceiling yield was measured and modelled [22,23]. The principles uncovered in these studies are fundamental to the way pastures are now managed in intensive pasture-based livestock systems.

Mass flux processes during regrowth were comprehensively described by Parsons *et al.* [23]. This analysis reconciled the apparent discrepancies in pasture herbage accumulation rates observed between continuous and intermittent defoliation by relating regrowth dynamics to LAI. Using the common sigmoidal pasture regrowth curve, Parsons *et al.* [23] showed how net instantaneous and average growth rates can be derived from this curve and used to identify the optimum time to harvest during the regrowth cycle to maximise herbage yield over repeated cycles of defoliation. The optimum is the point at which average growth (Equation (1)) reaches its maximum value during regrowth [14].

$$\text{Average growth rate} = (W - W_0)/t \quad (1)$$

where W = pasture mass at any time t during regrowth, and W_0 = pasture mass at the start of the regrowth period, also known as “residual” pasture mass.

Farmers cannot measure average growth rate. However, ecophysiological information provides an indicator that can easily be adopted by farmers, termed the “leaf stage” rule which is a measure of the readiness for grazing during regrowth from the plant perspective. Mass flux dynamics reveals that maximum average growth rate occurs at the point when the rate of senescence of old leaf material causes the instantaneous growth rate (Equation (2)) to fall below the average growth rate for the first time since the start of the regrowth period (see for example Figure 3.9 in [14]).

$$\text{Instantaneous growth rate (kg·DM/ha/day)} = dW/dt \quad (2)$$

where W = pasture mass and t = time, in units of one day

Tissue turnover studies (e.g., [22,24,25]) further reveal that the relative rates of new leaf growth and senescence of old leaf material are fixed by the pattern of leaf appearance and longevity on the ryegrass tiller. Perennial ryegrass is often termed a “three leaf” plant because it generally sustains a maximum of three live leaves on a tiller [26]. Hence, after grazing, once the third new leaf has been produced, the first leaf which was produced after grazing will start to die. The sequence of new leaf production and the death of older leaves is fundamental to the overall regrowth process. When the mass of old leaves that is dying and disappearing from the bottom of the pasture is equal to the mass of the new leaf being produced at the top of the pasture, the pasture reaches ceiling yield. New leaves are still being produced at this point, but the mass of new leaf added to the canopy is cancelled out by the mass of leaf that is dying and decaying: hence the net rate of pasture growth is zero. This will generally occur at, or after, three new leaves have been produced, unless the post-grazing residual is very low or very high, in which case it will occur later or earlier, respectively, as discussed below.

From this, Fulkerson and Donaghy [18] proposed that a simple assessment of the number of leaves produced since the previous grazing event carried out on a random sample of 10 to 20 tillers per paddock allows farmers to track plant physiological state during regrowth. They recommended that grazing be implemented when tillers have regrown between two and three new leaves since the previous defoliation, reasoning that this will provide the balance between rates of new leaf production, senescence of old leaves, maintenance of non-structural carbohydrate reserves to assist regrowth and plant survival during periods of stress required to maximise long-term pasture harvest rates. Subsequently, tools for farmers have been developed from this concept (e.g., [27,28]) and the leaf stage method has been adopted by dairy farmers in New Zealand, Australia, and Ireland.

In addition to assisting decision-making regarding when to graze during regrowth, the type of analysis performed by Parsons *et al.* [23] also helps define the optimum residual state to which pasture should be defoliated to maximise pasture harvest rates. They showed that when pasture is defoliated to a very low residual LAI, the initial rate of regrowth is retarded since the first leaf produced post-defoliation is restricted in size due to the limited amount of energy available to invest in the lamina of that leaf. Since leaf emergence rate and leaf elongation duration are relatively insensitive to defoliation severity within the range normally applied in farming systems [10], the plant is unable to compensate for the loss of C assimilation capacity (despite the mobilisation of carbohydrate reserves

plus changes in specific leaf area [11]) and the first leaf is necessarily restricted in size. Subsequent leaves are larger as C assimilation capacity increases and the full extent of compensatory effects (such as cessation of C export to roots to support new leaf growth [29]) is realised. In this situation, the point of maximum average growth will be delayed compared with a pasture where a higher LAI (and, therefore, a larger source of current assimilate for investment in new leaf growth) is left post-defoliation. Practically, the length of the regrowth cycle should be extended in response to severe defoliation to maximise pasture harvest, but the loss of yield incurred in the early stage of regrowth cannot be recovered and total pasture harvest over time will be less than for a system where a higher residual LAI is left.

Conversely, when a high LAI is left after defoliation, the rate of senescence will increase earlier in the regrowth cycle compared with a pasture where a lower LAI is left post-defoliation, since the residual LAI inevitably includes older leaf tissue nearing the end of its natural life. In this case, since the timing of maximum average growth rate is dependent on the relative rates of new leaf growth and senescence, it will be reached earlier, and the appropriate response in practice is to reduce the length of the regrowth interval to ensure yield is not foregone later in the regrowth cycle.

When translated into guidelines for farmers, these principles lead to the recommendation that pastures be grazed when between two and three new leaves have been produced since the previous grazing, or at approximately 2600–3200 kg·DM/ha pre-grazing pasture mass, leaving a spatially uniform residual pasture mass of between 1500 and 1700 kg·DM/ha [19,30]. Ideally, the rotation length (grazing interval) applied will be an emergent property of these rules as they are adapted to changing leaf appearance rates (e.g., [27]). In practice, it is often necessary to over-ride the theoretical optimum grazing interval to balance whole farm feed supply and demand over an annual cycle, for example ensuring that targets for the average amount of herbage mass across the farm are met at the beginning and end of each lactation [31]. This is an acceptable trade-off, provided farmers are aware they are “breaking the rules”, know why they are doing it, and know how to restore optimum grazing practices once the other needs have been met [32].

3.2. Opportunities for Improving Pasture Harvest Rates

The analysis above shows that, as well as tracking the accumulation of herbage mass during regrowth, the sigmoidal growth curve holds additional information that is valuable for improving the efficiency of grazing management. However, this information has seldom been used explicitly to test and further develop grazing recommendations. In part, this is due to the difficulty of accurately measuring the accumulation of mass during regrowth, given the temporal variation in growth conditions that typically occurs over periods of 3–6 weeks, the spatial heterogeneity in herbage mass that is ubiquitous in pastures (especially when grazed), and the relatively low precision of techniques for measuring pasture mass. Nonetheless, examples of sigmoidal regrowth curves can be found in the literature (e.g., [33–35]).

Figure 1 shows three regrowth curves for a perennial ryegrass pasture at Lincoln, Canterbury, New Zealand, areas of which were mown to residual pasture masses of 1150, 1500 or 1850 kg·DM/ha in early autumn (28 March). Before mowing, the pasture had been grazed as per “normal” farm practice: about 10–12 grazings per year, to a post-grazing residual between 1480 and 1750 kg·DM/ha. Relative to the pasture state maintained before the comparison was initiated, the three starting residuals represent over-grazing (1150 kg·DM/ha—hereafter called the “over” treatment), optimal grazing (1500 kg·DM/ha—“target”, as per the recommendations listed above), or under-grazing (1850 kg·DM/ha—“under”). The pastures were allowed to regrow for 45 days. At least once per week during regrowth, pasture mass was measured using a calibrated rising plate meter, light interception was assessed with a hand-held ceptometer, and leaf stage was monitored by counting the number of new leaves that had emerged since defoliation on a sample of 20 tillers per treatment. Pasture botanical composition and dead matter content were assessed 28 days after the start of the regrowth period, by hand dissection of four sub-samples per treatment cut to ground level.

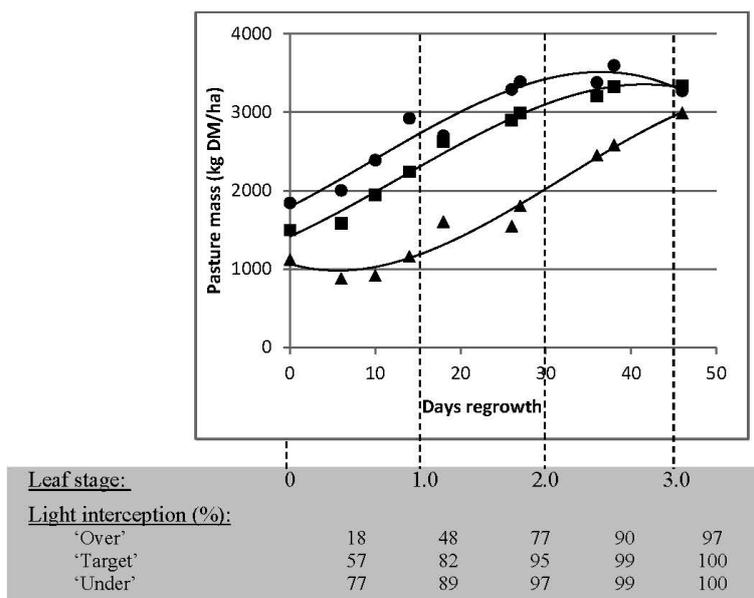


Figure 1. A single example of the regrowth of perennial ryegrass pasture following defoliation to three levels: 1150 kg·DM/ha (triangles, representing “over-grazing”), 1500 kg·DM/ha (squares, representing the “target” for residual state) or 1850 kg·DM/ha (circles, representing “under-grazing”) kg·DM/ha. Regrowth commenced on 28 March. Timing of the full emergence of the first, second and third new leaves after defoliation, and light interception, are shown below the x-axis.

During the regrowth period in April and May, rainfall was well above the long-term monthly averages, therefore plant available water was never limiting. The average daily air temperature was relatively consistent at around 11.5 °C, although day length was declining. The relatively favourable and consistent growth conditions meant that the data fitted the expected sigmoidal growth pattern. This is not always the case, and attempts to confirm the underlying ecophysiology with field measurements are often confounded by short-term variability in growth conditions. Also, the data presented in Figure 1 pertain to only one regrowth cycle in one environment. There is no implication in what follows that regrowth in all circumstances follows the classical pattern; rather, the intention is to show how the ecophysiological information presents opportunities to re-appraise grazing practices in the pursuit of improved pasture harvest efficiency, and thereby also increase farm profitability.

In this example, the interval between appearance of successive new leaves on tillers was consistent throughout the regrowth period at about 15 days. There was no difference between the treatments in the rate of leaf emergence, which is consistent with other, more-comprehensive studies [36,37]: unless grazing/cutting is extremely severe, the rate at which new leaves is produced is not affected, but the size (length, and weight) of new leaves can be reduced by severe defoliation [29,36]. Because leaf emergence rate was consistent across time and treatments in this example, the data illustrate how light interception, herbage accumulation and senescence change during regrowth, in accordance with changes in plant energy status. From this, it is possible to explore how management affects these interactions and estimate the costs in biological efficiency, and in profit per hectare, of failure to achieve the targets embedded in the recommendations listed above.

3.2.1. Targets for Residual Pasture State

In the example shown in Figure 1, ceiling yield of ~3500 kg·DM/ha was reached in the “under” and “target” treatments after about 38 and 45 days regrowth respectively. At this point, virtually all of the light available was intercepted by the pasture canopy (as shown by the numbers for light interception along the bottom of Figure 1). In the “over” treatment, net herbage accumulation in the first 15 days of regrowth when the first new leaf was produced was minimal, indicating that this first

leaf was much smaller than the first new leaf produced in the other treatments. After seven days of regrowth, only 18% of total light was intercepted by the pasture canopy in the “over” treatment, whereas in the “target” and “under” treatments, 57%–77% of light was being intercepted. Therefore, in the “over” treatment, plants had relatively little energy to invest in growing the first new leaf, and its size was restricted. As leaf size and light interception increased, the rate of herbage accumulation accelerated in this treatment such that the pasture approached ceiling yield after 45 days regrowth.

Parsons *et al.* [23] demonstrated that, to maximise the amount of pasture harvested per year in intermittent defoliation systems, the optimum time to graze during regrowth is the point when the maximum average growth rate of the pasture is reached. At this point, the optimum balance between the amount of new leaf being produced, and the amount of old leaf dying, has been reached. Going beyond this point means that the rate of leaf death increases and the efficiency with which further mass is added to the pasture declines. It is this declining efficiency which defines the maximum average growth rate as the optimal point to graze the pasture again.

Figure 2 plots the average growth rate for the “over”, “target” and “under” treatments shown in Figure 1. The arrows in Figure 2 indicate when maximum average growth rate is reached for the “under” and “target” treatments. The maximum average growth rate was reached after about 18 days in the “under” treatment indicating that to optimise pasture harvest when a high residual is left after grazing requires a relatively short grazing interval. The maximum average growth rate for the “target” treatment was reached about 30 days after regrowth commenced, whereas the average growth rate curve for the “over” treatment had still not reached a maximum after 45 days regrowth.

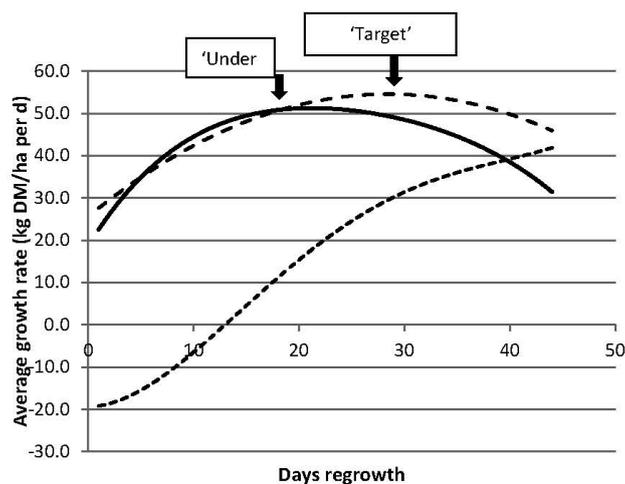


Figure 2. Average growth rate during regrowth for pastures mown to about 1150 (“Over”, dotted line), 1500 (“Target”, dashed line) or 1850 (“Under”, solid line) kg·DM/ha. Arrows indicate the point when the maximum average growth rate was reached during regrowth in the “under” and “target” treatments. The curves, and the point of maximum average growth rate, are derived from the fitted curves shown in Figure 1.

Importantly, the growth rate achieved at the point of maximum average growth rate is higher for the “target” treatment (about 55 kg·DM/ha per day on the vertical axis in Figure 2) than for the “under” treatment (about 51 kg·DM/ha/day; see also Figure 3.10 in [14]) although the difference is small. The total net amount of pasture grown at the point when maximum average growth rate was reached in the “target” and “under” treatments was 2110 and 1260 kg·DM/ha respectively, or an average of around 70 kg·DM/ha per day in both treatments. As noted above, maximum average growth rate was not attained in the “over” treatment: the highest growth rate reached was just over 40 kg·DM/ha per day, and after 45 days regrowth (the three leaf stage) pastures in this treatment had accumulated 2370 kg·DM/ha at a mean growth rate of 52 g·DM/ha per day. The “over” treatment can never catch up with the “target” treatment because of the lag in regrowth that occurred after defoliation

(Figure 1). This is fundamentally a problem caused by over-grazing (residual pasture mass/leaf area is too low). There is an important interaction here between the residual pasture state post-grazing and the length of the regrowth period; both of which can be controlled by grazing management decisions.

Continuing with the example shown in Figures 1 and 2 net herbage accumulation in the “under” and “target” treatments would be similar if the pasture were grazed again around the 2-leaf stage, but grazing after this point would result in relatively more herbage accumulating in the “target” treatment (Table 1). Conversely, net herbage accumulation in the “over” treatment would be much lower than in the “target” treatment if grazing occurred after two new leaves had emerged since the last grazing, but the gap between these treatments would narrow as the interval to the next grazing stretched out (Table 1). When averaged across the three scenarios shown in Table 1, the “under” and “over” treatments resulted in 240–465 kg·DM/ha lower herbage accumulation compared with the “target” treatment. Using the Dairy NZ Forage Value Index figure for the economic value (EV) of additional pasture grown in autumn in Canterbury (\$0.30 per kg·DM, [38]), this equates to between \$70 and \$140/ha potential profit foregone. This is the potential economic cost of missing the target range for the optimum residual state of the pasture. This loss will obviously compound if the target is missed frequently.

Table 1. Estimated effect of different regrowth intervals on the net amount of herbage accumulated (kg·DM/ha) during regrowth of pastures mown to about 1150 (“Over”), 1500 (“Target”) or 1850 (“Under”) kg·DM/ha residual pasture mass. Data apply to just a single regrowth event, in autumn, in Canterbury New Zealand, using the results shown in Figure 1.

Residual Pasture State	Timing of Next Grazing		
	2 Leaves (30 Days)	2.5 Leaves (37.5 Days)	3 Leaves (45 Days)
“Under” grazing	2095	2260	2065
“Target” grazing	2100	2440	2595
“Over” grazing	1415	1945	2375

How realistic are these estimates? Using cutting management applied to perennial ryegrass pastures from September to April, Lee *et al.* [39] measured about 1.2 t·DM/ha less pasture yield from pastures managed to a consistent residual of 1100 kg·DM/ha compared with a consistent residual of 1500 kg·DM/ha. This equates to around \$360/ha lost operating profit, based on an EV of \$0.30 per kg·DM. When cut to a consistent residual of 2300 kg·DM/ha, there was minimal effect on pasture yield. In a grazing experiment, Garcia and Holmes [40] observed a statistically significant 20% reduction in pasture growth from residuals of less than 1300 kg·DM/ha compared to residuals of greater than 1500 kg·DM/ha. Mean total annual pasture yields in their study were around 12 t·DM/ha; hence a 20% reduction in yield equates to around 2.4 t·DM/ha in lost feed production, or potentially \$600/ha lost operating profit. Similar to Lee *et al.* [39], Garcia and Holmes [40] did not observe any negative effect on pasture yield from higher pasture residuals of up to 2300 kg·DM/ha. The difference in herbage accumulation that emerges from the analysis of the regrowth curves in Figure 1 is not supported by these more-comprehensive studies but, as noted above: (1) the difference herbage accumulation over one regrowth cycle is relatively small; and (2) much depends on the interval between grazing that was applied because of the interaction that exists between post-grazing pasture state and regrowth interval. Nonetheless, negative effects of high residuals on pasture quality and sward structure would be expected, which could seriously restrict the efficiency of pasture utilisation and animal production. In the example shown in Figure 1, dead matter comprised 30% of the total pasture mass in the “under” treatment after 28 days regrowth, whereas it comprised only 12% of total mass in the “target” treatment and 2% in the “over” treatment.

3.2.2. Targets for Timing of Defoliation

When pasture regrows from a consistent post-grazing residual mass of between 1500 and 1750 kg·DM/ha, there is usually some curvature in the plot of herbage mass *versus* time (e.g., Figure 3), reflecting an increase in mass of the successive leaves. Using data from two years of a dairy grazing study where good control of pasture residual state was achieved, Chapman *et al.* [35] calculated that the first, second and third leaves produced after defoliation contribute 25%, 35% and 40% respectively of the total available pasture mass at the next grazing. This pattern is consistent with the theoretical analysis of Parsons *et al.* [23] which was further developed into the leaf stage grazing rule by Fulkerson and Donaghy [18], as described above. It provides a proxy from which the impacts of missing the optimum regrowth interval on the efficiency of pasture harvest, and farm profit, can be calculated without the need for empirical regrowth curve data. The only additional information needed to do this is average seasonal net herbage accumulation rates and leaf emergence intervals for a given environment.

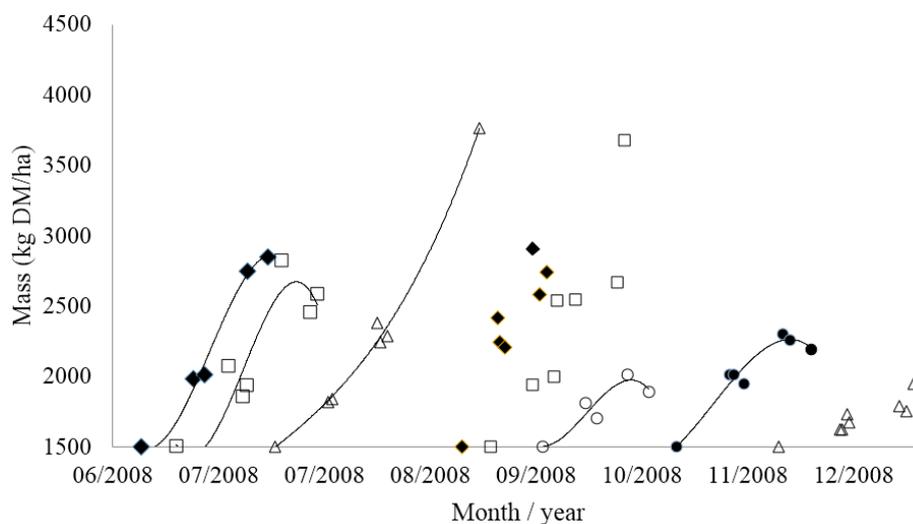


Figure 3. Regrowth curves for perennial ryegrass lamina tissue, derived from data for percentage of total tiller weight comprised by lamina, total herbage mass at the time of sampling, and observed leaf appearance rate data. Fitted lines are third-order polynomials, and are presented only where the polynomial described more of the variation in the data than a linear regression. From [35].

Table 2 shows the possible cost of erring towards a shorter regrowth interval (grazing at 1½ or 2 leaves) compared with a longer interval (3 leaves). It applies the 25:35:40 ratio seasonally (except for October–November, when reproductive growth is present and the difference in mass between successive leaves largely disappears [35]), along with typical pasture growth rates and leaf appearance intervals for irrigated dairy pastures in Canterbury. It also uses the DairyNZ Forage Value Index seasonal economic values previously described. The analysis shows that, for example in February–March, if growth rates are 55 kg·DM/ha per day, and the leaf appearance interval is 10 days, an additional 330 kg·DM/ha could be harvested if pastures were grazed at the three-leaf stage compared with the two-leaf stage. With an EV of \$0.25 per kg·DM, the total value for the season of the additional DM grown on the longer rotation is estimated at \$83. Across the full year, the analysis suggests around \$260/ha additional profit could be achieved using a longer defoliation interval, aligned with the three-leaf stage of regrowth.

Table 2. Estimated difference in dry matter grown and economic value (EV) of pasture for a dairy farm in Canterbury, New Zealand, where grazing occurs consistently at the 1.5 or 2-leaf stage of regrowth compared with the 3-leaf stage of regrowth.

Period	Growth Rate (kg·DM/ha/d)	Leaf Appearance Interval (d)	Contribution of 1st:2nd:3rd Leaves to Total DM (%) ¹	DM grown (kg/ha) When Grazed at			Difference in DM Grown (kg/ha)		EV for Season (\$/kg·DM) ²	EV of the Difference (\$/ha)	
				1.5-Leaf	2-Leaf	3-Leaf	1.5- v. 3-Leaf	2- v 3-Leaf		1.5- v. 3-Leaf	2- v 3-Leaf
February–March	55	10	25:35:40	2810	2970	3300	−500	−330	0.25	−125	−85
April–May	26	15	25:35:40	860	940	980	−120	−40	0.31	−35	−10
June–July	0			0	0	0	0	0			
August–September	34	15	25:35:40	1120	1220	1280	−150	−50	0.42	−65	−20
October–November	95	7.5	30:35:35	7200	7410	7550	−360	−140	0.29	−105	−40
December–January	95	10	25:35:40	4850	5130	5700	−860	−570	0.18	−155	−105
Totals				16,840	17,670	18,810	−1990	−1130		−485	−260

¹ From [35]; ² From [38].

Again, it is necessary to ask if these estimates are realistic. In Tasmania, Turner *et al.* [41] observed 20% greater herbage accumulation (18.0 *versus* 15.0 t·DM/ha) over 12 months when irrigated pastures were defoliated (using cutting) at the 3-leaf stage compared with the 1.5-leaf stage. This margin was consistent for the three different cultivars used in the study. The proxy approach shown in Table 2 predicts a 12% difference (18.8 *versus* 16.8 t·DM/ha) for pastures defoliated (by grazing) at the 3-leaf stage *versus* the 1.5-leaf stage respectively in Canterbury. These observations align well, and indicate that an additional \$260–\$480/ha in operating profit may be available for dairy farmers in Canterbury by consistently re-grazing at the point of maximum average growth rate (3-leaf stage) compared with earlier stages (2- and 1.5-leaf, respectively) of regrowth (Table 2).

3.2.3. Pasture Quality

One possible draw-back of this strategy is that the nutritive value of the feed eaten could be lower when pasture is grazed at the later stages of regrowth. It is well known that the composition of herbage of grass-dominant pastures changes during regrowth. As the leaves of both temperate and tropical grasses age, their digestibility declines due to increasing indigestible cell wall content and decreasing cell wall digestibility [41–44]. Thus, overall fibre content of herbage increases, while fibre digestibility declines, as regrowth proceeds. Countering these trends, grazing later in the regrowth cycle offers at least two advantages. Firstly, the crude protein (CP) concentration of old leaves is lower than young leaves meaning that the total CP content of grass herbage can be diluted by delaying grazing to later in the regrowth cycle [45–47]. The CP concentration of well-fertilised, ryegrass-dominant pastures frequently exceeds the concentration required to meet animal protein requirements [48]. Seventy to eighty percent of the excess N consumed is excreted in urine [49], resulting in high urinary N loadings in urine patches which provide a ready source of nitrate that can be leached below the pasture root zone eventually accumulating in receiving waters such as streams and lakes. In NZ and other temperate countries with intensive agricultural industries, this nutrient contamination of freshwater bodies is a significant environmental threat which is subject to increasingly stringent regulation at the source, the farm.

Secondly, the content of water soluble carbohydrates (WSC) increases during regrowth [46,50–52] with positive implications for the WSC:CP ratio of herbage and, hence, the efficiency of utilisation of protein in the rumen [53]. Furthermore, the expression of higher WSC content in cultivars bred for this trait is aided by a longer regrowth interval [54,55]. Therefore, changes in herbage composition associated with grazing later in the regrowth cycle can have positive benefits for managing some of the externalities of grassland farming. In this example, the effects of greater expression of the WSC trait and dilution of the total leaf CP concentration are additive and have been demonstrated to offer important potential gains in control of nitrate leaching [56].

3.3. Implementing Grazing Management on Farm

Considering the combined effects of over-grazing pasture and grazing too early in the regrowth cycle, as analysed in Section 3.2., it can be postulated that farmers could readily increase pasture harvest rates by 1–2 t·DM/ha per year and profit by \$300–600/ha per year through accurate implementation of well-documented grazing decision rules. Of course, such benefits will only be realised if optimal grazing targets are currently not being achieved on-farm. Despite a long history of focussing on grazing management and a reputation for achieving high levels of pasture utilisation on New Zealand dairy farms, there is evidence of wide variation in grazing management practices with potentially large negative consequences for pasture productivity. In a study where pre-grazing pasture mass, leaf stage and post-grazing pasture mass were measured every two weeks on seven dairy farms in the lower North Island, New Zealand for 10 months, McCarthy *et al.* [6] observed that 49% of grazing events occurred at or before the 2-leaf stage, and only 27% occurred between the 2- and 3-leaf stage. The recommended post-grazing herbage mass target was achieved in only 48% of grazing events,

with individual farms showing a tendency toward consistently either under-grazing or over-grazing relative to the target.

It must be noted that, on seasonal calving dairy farms that rely mostly on pasture for feed, there are times of the year when the theoretical best practice for management of pasture regrowth does not result in the optimal overall outcome for the farm system. For example, the application of long regrowth intervals in late autumn and winter when pasture growth rates are relatively low helps to increase average herbage mass across the farm and ensure sufficient pasture is available to bridge the feed gap between calving and the acceleration of spring pasture growth [31]. Here, extended regrowth intervals are implemented via strip grazing of paddocks at a time when cows are not lactating and can be fed a restricted diet sufficient to maintain, or achieve modest increases in, body condition score. The result is that some of the feed grown in late autumn or winter (a period of relatively low feed demand) is “transferred” to late winter-early spring (a period of high feed demand, but variable and often low pasture growth). In many situations, this will result in low post-grazing herbage mass on grazed strips, and push regrowth beyond the 3-leaf stage on strips that are withheld from grazing for long periods (up to 100 days): however, the “cost” of doing this is generally less than the cost of purchasing supplements to fill the early lactation feed gap, therefore overall farm profit is improved. This is an example of a situation where the “rules” of best management for regrowth can be bent for a good reason [32].

The effects of these management practices will be reflected to some extent in the survey findings referred to above [6]. Nonetheless, the results indicated that there is substantial room for improvement in grazing management on New Zealand dairy farms, and prompted (among others) two responses. Firstly, a renewed focus on the fundamental principles of grazing management emerged in extension material distributed to all New Zealand dairy farmers (e.g., [7]). Secondly, recognising that part of the problem is related to relatively low adoption of pasture monitoring practices such as weekly assessment of pasture mass in each paddock and the generation of a whole-farm feed profile for assisting short-term grazing management decisions (e.g., [57]), farm system simulation was used to estimate the profit foregone as a result of having incomplete information on which to make pasture allocation decisions. This analysis [58] showed that, compared with a situation where no information was available for the herbage mass of individual paddocks, farm operating profit could be increased by about \$385/ha per year if pasture mass was measured for each paddock each week, even if the error associated with the measurement was $\pm 15\%$. That is, having some information is substantially better than having no information. The profit gains estimated by Beukes *et al.* [58] are similar to those arrived at in the analysis in Sections 3.2.1 and 3.2.2 above. Both approaches point toward large gains in profit being available in many New Zealand dairy farms by application of well-proven management practices that have strong ecophysiological foundations.

4. Future Opportunities for Application of Ecophysiological Information

4.1. The Extended Ryegrass Phenomenon and Its Implications for Grazing Management Practices

One objection to the idea of implementing longer regrowth intervals (as discussed in Section 3.2, above) is that the pasture mass at the time of grazing will be greater, making it more difficult for animals to graze down to the target residual pasture state. Grazing management recommendations developed in the NZ dairy industry in the 1970s and 1980s emphasised the need for high stocking rates to control pasture residual state and maintain high feed quality (e.g., [4]). At this time, many dairy pastures were likely based on old ecotypes of perennial ryegrass. Pasture renewal rates were low, and cultivar choices were restricted to a handful of mid-season flowering types with strong winter and spring growth, and relatively poor summer growth. They were also characterised by relatively high sheath/pseudostem to leaf ratios which would have posed a sward structural barrier to grazing into the lower sward layers [59]. Irrespective of whether pastures were old or recently renewed, the ryegrass populations in them would have been highly infected with the “standard” or “wild type” ryegrass

endophyte *Epichloë festucae* var. *lolii* (formerly *Neotyphodium lolii*, [60]). This endophyte produces high concentrations of the alkaloids lolitrem and ergovaline, especially in the summer/autumn dry conditions of northern New Zealand [61,62] where the majority of New Zealand's dairy cows were farmed. These alkaloids are concentrated in the base of the leaf sheath. They induce aversive responses in ruminants, which probably limit grazing intensity, *i.e.*, it was necessary to "force" animals to graze low into the canopy. Hence, high stocking rates were necessary to "graze out" pastures effectively.

The influence of the practical guidelines for grazing that were developed in the 1970s and 1980s can still be seen in current grazing management recommendations, for example in the guideline that pre-graze pasture mass does not exceed 3200 kg DM/ha. Yet the types of pastures used for milk production today are markedly different. Firstly, very few "old" pastures now remain in the industry, after farming has intensified in the traditional areas and expanded into non-traditional areas mainly through the conversion of sheep and beef farms to dairying. The latter change in land use has always been accompanied by pasture renewal. Secondly, the role of endophytes in the ecology of grazed pastures is now well-documented [63–65] and endophyte strains that do not produce the alkaloids that are toxic to animals have been commercialised [64]. Thirdly, the genetic diversity of cultivars available in the NZ market is now much greater [66]. Breeding objectives during the 1990s and 2000s emphasised later flowering [67], using Mediterranean germplasm and polyploidy to delay maturity, reduce the magnitude of the traditional mid-spring peak in growth, and increase growth rates in summer and autumn. Some of these traits, especially tetraploidy, are well-documented as facilitating greater dry matter intake [68] allowing better control of post-grazing sward state. Milk production benefits are likely from the use of such material [69], but this has not yet been confirmed in rigorous grazing systems experiments [70].

More targeted research is needed to quantify exactly how different modern cultivars are compared with older cultivars in terms of grassland productivity [70], and therefore some caution is required in when questioning whether current guidelines still result in best possible pasture harvest rates. Nonetheless, the emergence of greater genetic diversity through the development of an "extended phenome" of perennial ryegrass (combining genetic variation in the ryegrass plant and the endophytic fungus) may open opportunities for farmers to grow and utilise more pasture, thereby controlling the costs of milk production by reducing/avoiding the need to purchase expensive supplements. This opportunity has not yet been investigated in targeted research, even though the theoretical and practical bases by which it can be realised are well-documented (as described in the previous section). One of the barriers is the absence of quantitative information on the amount of phenotypic variation in specific shoot traits that exists in current perennial ryegrass cultivars, and their impact on grazing efficiency, animal intake and milk production. Ecophysiological explanations for the effects of management and environment on the traits and processes of interest are essential. This information must be allied with field-scale grazing studies to provide the information that farmers require to correctly match genotype, management and environment for better biological efficiency and profit. Early inroads are being made into this field. For example, Wims *et al.* [71] identified an important interaction between cultivar and growth stage (vegetative *versus* reproductive) which influenced relative milk production of dairy cows and concluded that sward structural differences between cultivars are more important during reproductive development, while differences in digestibility are more important during vegetative growth. There is more to be learnt in this field of plant phenotypic variation and pasture-animal interactions, which offers gains for pasture-based livestock producers in all temperate regions.

4.2. Pasture Persistence

As the intensification and expansion trends in the New Zealand dairy industry described above have proceeded, a growing concern has emerged regarding the persistence of newly sown pastures. This issue was the subject of a special symposium held in 2011 [72] to review the state of knowledge regarding the extent, seriousness, and causes of the problem. The symposium clearly demonstrated

that it is a multi-faceted problem, involving many interacting causal factors which can be broadly grouped under the headings of environment, management and genetics (perennial ryegrass plus fungal endophyte). The symposium also highlighted how little is known about the underlying plant growth and population processes that are likely to be involved. This is surely a prime opportunity for ecophysiological research: for, as with the example discussed in the previous section, ecophysiological information is critical to the solution.

Unravelling the problem first requires a clear definition of what is meant by “persistence”. Parsons *et al.* [73] argued that it is best defined as the persistence of the expected yield advantage of a new pasture compared with the pasture that was in place before. In this context, “poor persistence” is not just a function of physical survival of plants of the sown species/cultivar but can also be caused by changes in the expression of yield traits over time which erode early advantages. From the perspective of ecophysiological investigations, this broader view of the problem invokes the need for: agronomic information on the relative yields of “old” and “new” pastures to define when there is a persistence “failure” and the magnitude of the failure; well-constructed control treatments (both positive and negative) so that the incidence of persistence failure can be confirmed; a stronger focus on the fundamental plant traits, rather than on the cultivar (given that there is strong overlap between cultivars in traits which frequently confounds attempts to elucidate key factors); and more emphasis on community and ecosystem processes to complement the traditional whole-plant focus of ecophysiology.

In the case of pasture persistence, previous research into the problem has addressed only some of these requirements, creating difficulties in pin-pointing critical processes and reconciling apparently conflicting results. Often the focus has been on ryegrass tiller density in pastures as an indicator of persistence. However, the existence of a relationship between tiller density and the persistence of an expected yield advantage has not been proven, apart from the obvious situation where perennial ryegrass populations are eliminated by, for example, major insect pest damage to pastures lacking the protection available from novel endophytes in regions vulnerable to pest outbreaks [74]. More progress has been made in relating changes in ground score [75] to trends in dry matter yield of ryegrass cultivars in Ireland [76]. Ground score change has subsequently been incorporated into the Irish Pasture Profit Index which ranks ryegrass cultivars according to their economic worth [77]. Similar information for New Zealand cultivars and their yield trends is not available, although initial analysis of one long-term data set comparing yields of 25 perennial ryegrass cultivars over 8 years in a summer-dry environment indicates no relationship between ground score and long-term yield differences [78].

At the population level, it is obvious that persistence is dependent on maintenance of a population of tillers. Individual tillers have a finite life span [79] so it is logical to look for tillering traits that might explain why some pastures “persist” better than others. However, for the density of a population of perennial ryegrass to remain stable, each tiller need leave only one replacement [80]. Perennial ryegrass is quite capable of doing this, since plants can rapidly initiate new tillers under favourable conditions [10,81]. There is no evidence that failure to replace tillers that die naturally or in response to short-term growth stresses, limits ryegrass “persistence” in temperate regions where soil moisture deficits are absent or relatively mild and/or short in duration [82].

Well-targeted ecophysiological research remains critical to resolving the pasture persistence problem. However, the discussion above highlights that it must be closely-aligned with agronomic investigations (so that, for example, yield differences in response to treatments can be confirmed, and plant characteristics can be related to differences in pasture yield), and genetics/genomics (so that the focus can shift to traits, rather than cultivars, and opportunities for identifying markers for persistence can be exploited). There is also a distinct gap in knowledge of what changes, if any, occur in the genotypic and phenotypic structure of ryegrass populations over time, how fast those changes occur and what traits they favour (the direction of change) and, indeed, if these changes ultimately have any bearing on the persistence of yield. Hence, stronger connections between ecophysiology and population ecology are also needed.

5. Conclusions

The discipline of plant physiological ecology is fundamentally important for the advancement of the biological efficiency and sustainability of pasture-based livestock systems throughout the world. Ecophysiological information has already contributed to the development of important management guidelines and tools that are used by farmers in temperate regions. Several opportunities for further developing those guidelines and tools are available using the existing body of ecophysiological information: if taken, those opportunities will allow farmers to increase pasture harvest rates at little extra cost and therefore support improvements in farm profit.

By contrast, ecophysiological information has made less of a contribution to gains in forage plant breeding, even though several credible routes have been proposed (as reviewed by [74]). Closer links between ecophysiology and plant genetics/genomics (including population genetics) will help focus effort on the right traits and determine when/if meaningful progress is being made. These two discipline areas are naturally aligned, but seldom deployed together. Likewise, the horizons for ecophysiology also need to encompass well-constructed agronomic investigations, as well as farm systems experimentation and systems modelling. There are few examples where the links between these various disciplines have been forged. Until these types of links are developed, progress in improving the efficiency of pasture-based agriculture will be limited, and the discipline of ecophysiology may struggle to retain its relevance.

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