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Review

Defoliation, Shoot Plasticity, Sward Structure and Herbage Utilization in Pasture: Review of the Underlying Ecophysiological Processes

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Abstract: Sward structure affects herbage growth, pasture species dynamics, and herbage utilization. Defoliation management has a major impact on sward structure. In particular, tiller size-tiller density compensations allow for the maintenance of herbage growth. Tiller size and tiller density are determined by several major morphogenetical components. Defoliation affects these morphogenetical components, depending on its frequency and its intensity, through several direct and indirect physiological and environmental processes. Due to the implications of leaf area removal, defoliation has a direct effect on the mobilization of C and N reserves and their supply to growing leaves. In addition, defoliation has an indirect effect on leaf and tiller morphogenesis, due to its impact on the light environment within the canopy as well as plant responses to light signals (blue light, red far red ratio). Defoliation may also in some cases have a direct negative effect on leaf growth by damaging leaf meristems. Understanding the respective role of these various physiological and environmental processes requires studies where defoliation, photosynthetic active radiation and light signals are manipulated independently. Past and recent knowledge on these direct and indirect effects of defoliation on plant morphogenesis are discussed, leading to an overall integrated view of physiological and environmental processes that lead to adaptations of sward structure in response to defoliation management. Major consequences for herbage utilization efficiency are presented.

Keywords: sward management; defoliation; leaf growth; tillering; light; grasses

1. Introduction

1.1. Plasticity of Sward Structure in Relation to Defoliation and Sward Management

Plant-herbivore relationships have been the subject of numerous earlier studies. These studies have shown that plants and swards have the capacity to adapt their structure (plasticity in size, number and spatial orientation of shoot organs), productivity and persistency, to the defoliation characteristics that result from grazing or cutting management strategies [1–3]. The plasticity of sward structure in response to successive defoliations mostly results from compensations between tiller size and tiller density. Swards that are frequently defoliated (under intensive continuous grazing management, for example) have a higher density of smaller shoot axes (tillers, branches) and conversely, swards that are defoliated infrequently (under a cutting regime, for example) have a lower density of larger shoot axes [3]. Moreover, earlier studies have also shown that the plasticity of sward structure in response to defoliation not only allows adaptation in sward productivity but also partly determines herbage utilization by animals, in conjunction with animal grazing behavior [4–9]. For a similar herbage mass, swards with a higher lamina/sheath (grasses) or leaf/stem (dicots) ratio allow a higher intake than swards with a higher sheath, pseudo-stem or stem ratio [7,10]. Maximal daily intake is related to tiller size, the vertical profile of bulk density, which depends on tiller density, and sheath length, which limits grazing in the lower sward layers [6,8,11,12]. The plasticity of sward structure in relation to defoliation and grazing management, together with the impact of sward structure on herbage utilization of grazing animals, are probably responsible for the observation that within certain limits in defoliation management, herbage productivity and herbage utilization by grazing animals are maintained at a comparable rate, despite variations in herbage mass [13].

1.2. Understanding Sward Structure Plasticity: The Need for Integrating Physiological and Environmental Processes

Although it is recognized that plasticity of sward structure plays a major role in the capacity of swards to adapt to defoliation and grazing management, the underlying ecophysiological basis, *i.e.*, integration of plant physiological and environmental processes at the community level, are still poorly understood [14]. This lack of knowledge becomes even more critical when we want to consider and address the plasticity of multispecific sward communities, where specific species responses determine sward dynamics and species equilibrium. Improvement in this area of knowledge would allow a better definition of the potential and limits in the adaptability of sward structure to management [15], and would therefore help to define strategies and conditions allowing grassland sustainability. The objective of the present paper is to give an overview of the current knowledge on the processes underlying plant and sward plasticity in response to defoliation, and to highlight recent findings. For simplicity, the exercise is limited to grasses, but it could be conducted similarly on several dicots, particularly white clover, with almost similar conclusions supported by an almost similar literature background.

An earlier approach of sward structure and herbage productivity and utilization focused on the relationship between leaf area index (LAI) and growth rate. The net herbage accumulation rate is generally considered maximum for an LAI in the range of 3–5 [3,16–18]. At a lower LAI, net growth rate is limited by light interception and at a higher LAI, net growth rate is limited both by the burden of respiration, particularly respiration of shaded organs at the bottom of the canopy, and by the loss of plant material through senescence and litter fall. In addition, intake by animals of ageing and senescing organs is limited [4], and therefore at high LAI, not only net herbage productivity but also herbage utilization is restricted. However, this earlier analysis, based on the LAI-growth relationship, is derived from the study of swards under discontinuous defoliation (cutting), and needs to be adapted to conditions of continuous grazing [16], where long-term sward structure adaptations modify photosynthesis-respiration-senescence relationships.

An alternative approach has been proposed [3,18,19], in which tissue flows and tissue turnover in the sward are analyzed through several growth components at a plant axis (tiller or branch) level: leaf appearance, leaf growth and leaf senescence rates, branching pattern, and specific organ mass. By definition, this approach is closer to sward structure analysis than the previous approach relying on LAI and growth rate. Therefore, most of the current knowledge related to the previously mentioned tiller size-tiller density compensations occurring during adaptation of sward structure to defoliation management is derived in some way from the tissue turnover approach. In fact, these two approaches are complementary, since LAI is both an input of the former (growth rate model) and an output of the second (tissue turnover) approach.

In the first instance, sward LAI can be decomposed into:

$$\text{LAI} = \text{Tiller density} \times \text{Leaf Area per tiller}$$

Tiller density and leaf size are negatively correlated. The inverse relationship between tiller density and tiller size (size density compensation, SDC) has been described for many grazed swards [3,20]. Attempts have been made to relate the slope of the SDC line obtained under various grazing intensities with that of the self-thinning law, *i.e.*, −3/2 in log/log scale [21]. However, as demonstrated in [22], the −3/2 slope occurs only when LAI has reached a maximum value corresponding to the environmental potential of the sward. In continuously stocked swards, LAI depends on defoliation intensity and does not often reach its maximum value. As a consequence, the SDC slope is steeper than −3/2, and is then often close to −5/2 [23–25].

Studying the tiller density-tiller size relationship clearly provides an experimental way to evaluate the impact of defoliation regimes on herbage growth and allows the delineation of situations where the compensation may or may not be effective. However, the underlying processes that drive and allow (or not) this compensation are not explicitly identified. For this purpose, a more detailed and dynamic analysis of plant axis growth and branching is necessary. Such an analysis was initiated earlier [18], but new knowledge is now available and allows a finer understanding of the involved processes.

2. Defoliation Patterns, Sward Structure and Light Environment

2.1. Defoliation Patterns in Relation to Sward Management

Defoliation basically consists of removing part of the shoot organs of plants and is primarily characterized by its intensity (or severity) and its frequency (or its inverse, the defoliation interval). In several instances, defoliation also needs to be characterized by additional parameters, such as its spatial heterogeneity or its timing in relation to plant development, particularly floral initiation. On a tiller basis, the defoliation interval usually varies from low values, typically 7–15 days under intensive continuous grazing management and depending on the stocking density [6,12,26,27], to intermediate values of approximately 20–30 days in rotational grazing, and to high values of approximately 30–60 days in cutting systems. The tiller defoliation interval may reach higher values in extensive systems or where a long rotation is used to stockpile feed. In such situations, the impact of defoliation mostly becomes a question of biomass accumulation and its negative impacts from both plant and animal points of view. Under intensive management, defoliation intensity is generally higher under long than under short defoliation intervals. The defoliation intensity may involve over 80%–90% leaf area removal under mowing depending on the cutting height. In rotational grazing, defoliation intensity depends on the stocking density and the duration of the grazing period, which determine the residual sward height. As demonstrated in [6], a single tiller is defoliated several times during the grazing process. As a result, the intensity of defoliation in rotational grazing may vary between 50%–75% depending on grazing management. Under continuous grazing, the defoliation intensity of individual tillers, expressed on an extended tiller length basis, was found to be 35% per tiller with dairy cows [5]. It varied in the range of 40%–60% on the basis of individual leaf length [27,28]. This defoliation intensity is similar to the defoliation intensity measured in a rotational system for a single defoliation event [5,28]. From a plant physiology perspective, as well as from a sward structure point of view, it is important to note that the recently expanded leaves, located in the upper layers of the canopy, are generally defoliated more frequently and to a larger extent than older leaves, as shown under sheep grazing [27,29].

2.2. Plant Morphogenesis is the Driver of Sward Structure, Plasticity and Adaptation to Management

Since leaf area is a major determinant of plant growth and since defoliation leads to the removal of part of it, adaptation of sward structure to defoliation management has to be analyzed first in terms of leaf area dynamics. Moreover, since the plasticity of sward structure in response to defoliation operates in terms of tiller size-tiller density compensation, the dynamic fluctuation of leaf area has to be analyzed on a tiller (or more generally on a plant axis) population basis.

The leaf area index of a sward is determined by 3 morphological components: (i) leaf area (often approximated in grasses by leaf length due to the linear shape of their lamina); (ii) number of mature leaves per tiller; and (iii) tiller density. A similar sward LAI can be obtained by different combinations of these components. As underlined in [18], these components result from the morphogenetic activity of tiller populations, and have to be analyzed accordingly.

In a vegetative sward, tiller morphogenesis can be described by three main variables (Figure 1): (i) leaf appearance rate (LAR); (ii) leaf elongation rate (LER); and (iii) leaf life span (LLS). These components are genetically determined and are influenced by environmental variables such as temperature, nutrient supply and plant water status, and additionally by defoliation through induced changes in light interception and light quality (see next paragraph). Leaf size or leaf length (LL) can be considered as the ratio between LER and LAR, considering that for a given genotype, the leaf elongation duration (LED) is proportional to the leaf appearance rate LAR [30]. The maximum number of green leaves per tiller (NL) can be considered as the product of LAR and leaf life span (LLS). Tiller density can be analyzed through tiller appearance and tiller death rates.

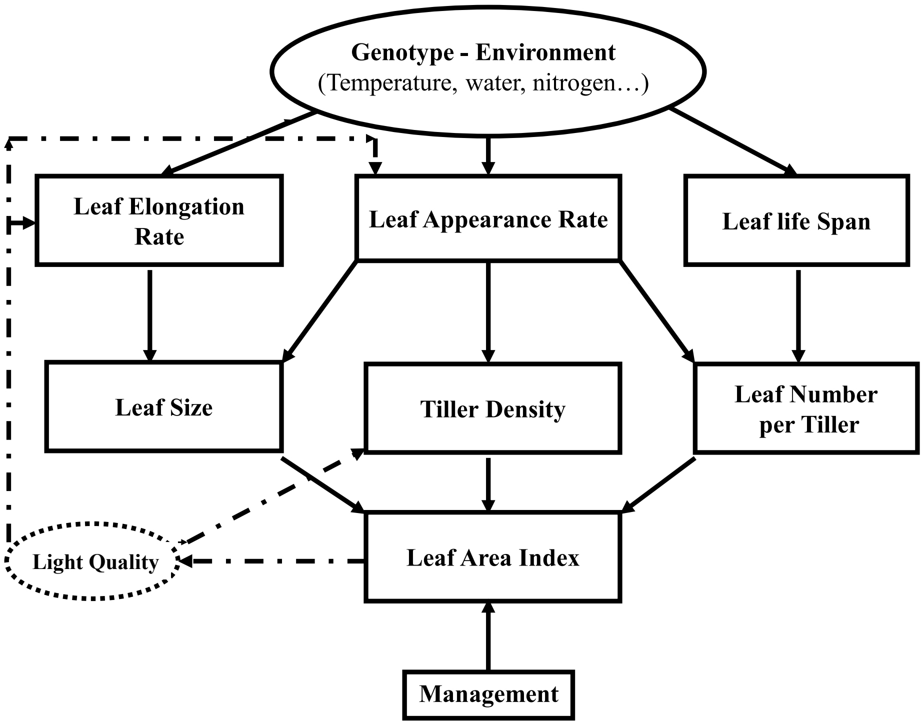

Figure 1. Determination of the grass sward structure in relation to components of shoot morphogenesis. Adapted from [18].

A number of sward structure parameters other than leaf area are also relevant with respect to the impact of defoliation on herbage growth and utilization. In particular, length, vertical orientation and horizontal dispersion of pseudo-stems (sheath) or stems partly determine tiller access to light under plant competition, and also partly determine herbage accessibility to mowers or grazing animals. The stage of floral induction of the apical meristem determines the short-term survival potential of grazed tillers since the probability of apex decapitation increases with the apex elevation within the sheath tube in reproductive tillers.

2.3. The Role of Light Signals in Plant Responses to Defoliation

The direct role of defoliation (*i.e.*, decreased light interception due to leaf area removal and subsequent decreased rate of plant photosynthesis) in tiller morphogenesis will be discussed in detail below. However, in addition to its direct role, defoliation also has a major impact on the spectral composition of light within the sward, which in turn also affects tiller morphogenesis to a major extent and thus sward structure. Besides its role in plant photosynthesis, light also impacts plant morphogenesis as a source of light signals [31–34].

Several photoreceptor families have been identified in plants, in particular phytochrome and cryptochrome families, which are responsible for morphological responses to the red far-red ratio (R/FR) and to blue radiations (Bl), respectively. Due to a higher absorption of R than FR by leaves, foliage reflection and transmission of FR is larger than foliage reflection and transmission of R. Therefore, in the vicinity of plants and during sward development and associated leaf area index (LAI) increases, the R/FR ratio decreases within and below the canopy, and light may even be enriched in FR compared with incident light. Considering these modifications in FR light and the R/FR ratio in the plant environment, and considering that plants have the ability to morphogenetically respond to the R/FR ratio, it has been proposed [35–38] that FR (or alternatively the R/FR ratio) acts as an early signal of competition for light within canopies. This signal triggers shoot morphogenetic responses, anticipating mutual shading and reducing its consequences on plant photosynthesis. The signaling role of blue radiation operates differently than R/FR. Cryptochrome responses are observed over most of the blue light domain [39]. In addition, absorption of blue light by foliage is similar over most of the blue domain, so that gradients in blue light in the plant environment are parallel to gradients in photosynthetic active radiation (PAR). As a consequence, blue light is not generally considered as a competition anticipating light signal, in contrast with the R/FR ratio. However shoot morphogenetical responses to blue are significant and differ from responses to PAR, both in terms of physiological processes and morphological impact [40–44]. Therefore, they participate, in conjunction with responses to R/FR, in the morphological plasticity of plant swards.

Experimentally, the delineation between the direct role of defoliation (decreased plant photosynthesis due to leaf area removal) and its indirect role in the light environment (modification of both photosynthetic and morphogenetically active radiation) requires the analysis of the responses of isolated plants to various independent combinations of defoliation regimes and light quantity and quality supply. Care must be taken in the interpretation of most previous light intensity studies since in many instances, manipulation of light intensity was associated with an uncontrolled modification in light quality.

3. Defoliation Patterns, Light Environment and Dynamics of Sward Structural Components

3.1. Leaf Appearance Rate

Defoliation sometimes appears to negatively affect LAR [45–47]. However, in several instances, the effect of defoliation on LAR is very limited or not significant [48,49], or defoliation may even increase LAR [50]. Light intensity has been found to have a positive effect on LAR in some instances [49,51], or to have a limited effect on LAR in others [52–54]. Although very few studies are devoted to the effect of light quality on LAR, in comparison to studies on the effect of visible light, it appeared for *Lolium perenne* and *Festuca arundinacea* that LAR is not significantly affected by the R/FR ratio or by blue light [49,55]. Therefore, the positive effect of light intensity on LAR that was observed in some circumstances can be interpreted as been mediated by increased photosynthetic activity and carbon supply rather than by light signals.

A number of studies show that independent of the impact of defoliation or light intensity and quality, the LAR of successive leaves of a tiller decreases during its development. This ontogenic decrease in LAR is observed similarly in plants grown from seedlings [56–61] and plants recovering from defoliation [62,63]. These studies show that the LAR of successive leaves may decrease by a factor of more than 2 during plant development, and that the decrease in LAR is systematically associated with an increase in sheath and lamina length (Figure 2A). As suggested in [64], the length of the sheath tube of older leaves may affect the LAR of the younger growing leaves. The previously mentioned ontogenic decrease in LAR during plant development may therefore be related to the ontogenic increase in the sheath length of successive leaves. The increase in sheath length over successive leaves tends to increase LAR due to the increased distance for a leaf to emerge to light. However, it was shown that this effect contributes to the decrease in LAR to only a limited extent [60]. Thus, the decrease in the LAR of successive leaves is probably more related to a profound modification of the structure of the leaf growth zone and underlying cellular division and extension processes. The shortening of the sheath by defoliation should at least partly reverse the ontogenic increase in sheath length and the decrease in LAR of successive leaves of undefoliated plants. However, in addition, the LAR of defoliated plants may also decrease due to a shortage in carbon supply to the growing leaf. These superimposed opposite effects may explain the contradictory results reported in the literature, and particularly the observation that LAR may be accelerated under a severe compared to a lax defoliation regime [48,50].

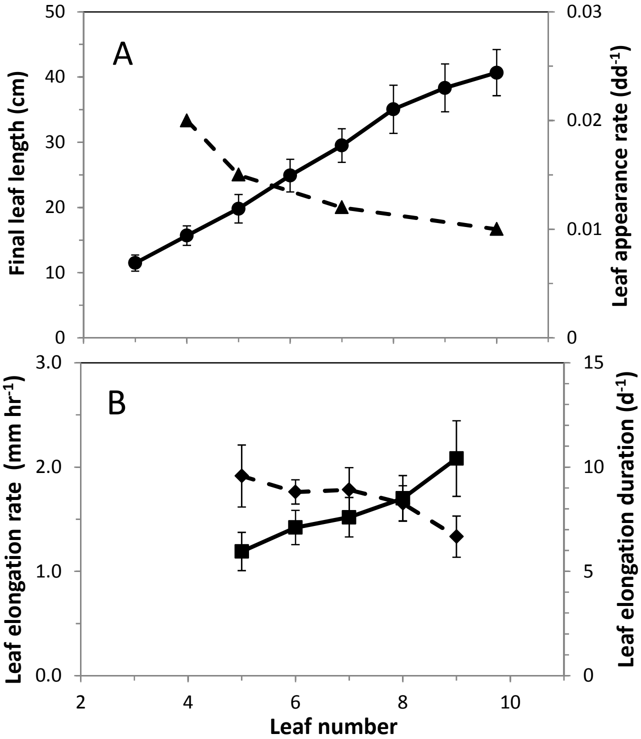

Figure 2. Leaf growth components (appearance and elongation rates, elongation duration, final length) of successive leaves on the ryegrass (*Lolium perenne*) main tiller of undefoliated plants. (**A**) ●: final leaf length; ▲: leaf appearance rate; (**B**) ♦: leaf elongation rate; ■: leaf elongation duration. Plants were grown under constant controlled conditions. Redrawn and completed from [61].

While LAR has long been considered to be independent of tiller ontogenic development, recent studies show that this is not the case. The ontogenic decrease in LAR is substantial and needs to be taken into account to understand the dynamics of sward structure, particularly because of its implications for tillering (see Section 3.4).

3.2. Leaf Growth Rate

For many years, the physiological effect of defoliation on leaf growth and LER has been primarily considered as the result of a decrease in plant photosynthesis, induced by leaf area removal and therefore by a larger dependency on carbohydrate reserves. The numerous studies aimed at manipulating non-structural carbohydrate levels and evaluating leaf elongation or growth have shown that following defoliation, leaf growth is affected by the non-structural carbohydrate level only below a certain level [3]. However, the critical level of non-structural carbohydrates varies according to growing conditions, including air CO_2 concentration [65], and thus a general threshold value cannot be defined. Since these early studies on non-structural carbohydrates and LER, it has become more clearly understood that plants are able to maintain leaf elongation, following defoliation, through a number of physiological and morphological transient adaptations, reviewed in detail by [66] and presented more briefly below. These various physiological adaptations explain why leaf growth is not necessarily correlated with the non-structural carbohydrates level.

Following defoliation, the specific leaf area of new leaves or new leaf segments often increases [47], leading to a lower cost in C and N related to leaf area expansion. The increase in specific leaf area probably occurs from both a lower accumulation of soluble carbohydrates and from changes in leaf structure (width, thickness), as suggested by [67], and occurs under low irradiance [68,69]. However, the extent to which these structural adjustments occur following defoliation would need clarification. Non-structural carbohydrates (mostly fructans in C_3 grasses) and nitrogen compounds accumulate at relatively high concentrations in leaf intercalary meristems of grasses, and transiently participate in providing C and N to support leaf growth after defoliation [67,70–74]. Non-structural carbohydrates and nitrogen compounds from mature shoot organs left intact following defoliation generally provide the quantitatively major source of C and N mobilization to support new leaf growth [75–82]. However, increasing defoliation severity by decreasing the amount of intact shoot tissue increasingly compromises C and N mobilization potential to sustain new leaf growth. Root mobilization of carbon and more importantly nitrogen may also occur when mobilization from shoot organs is insufficient. In grasses, fructans do not accumulate to a large concentration in the mature zones of roots, and it remains unclear whether their remobilization provides substantial C supply to leaf growth or whether they are mostly used for root respiration as shown for root starch in *Medicago sativa* [83]. Root N and possibly C mobilization to shoots may be accompanied by a significant decrease, and in some cases an almost complete cessation of root growth, and may also induce root senescence ([84] and references therein). In addition to supplying nitrogen to sustain leaf growth, mobilized N compounds, essentially amino acids, also provide a substantial amount of carbon [85]. Although no definitive arguments have been made with respect to whether post defoliation leaf growth is predominantly limited by carbon or by nitrogen, recent studies suggest that C and N co-regulate leaf growth in general [85], and thus either C or N may play the predominant role depending on prevailing conditions in nitrogen supply and PAR prior to defoliation. Recent studies clearly show that the dependence of leaf growth on non-structural carbon accumulated prior to defoliation is shorter (about 2 days) than previously thought [85,86].

However, these physiological mechanisms, which allow maintenance of a significant leaf growth rate following defoliation, have limits. These limits need to be evaluated to properly understand the impact of defoliation management on leaf elongation. Under repeated defoliation, the physiological and morphological adaptive mechanisms are not necessarily sufficient to sustain the leaf growth rate. During sequences of weekly defoliation, leaf elongation of *Lolium perenne* is substantially and durably altered after the second to the third defoliation event (Figure 3A). In parallel, the non-structural carbohydrate concentration decreases and remains at low values (Figure 3B) unless defoliation pressure is suppressed, resulting in non-structural carbohydrate concentration and LER recovery. This illustrates that under repeated and frequent defoliation, carbohydrate reserves may not re-accumulate to a sufficient level between two consecutive defoliations and therefore may reduce LER, as confirmed in other studies [87–90]. These observations on isolated plants are in line with field data on tall fescue under continuous sheep grazing, showing that the LER of grazed tillers was substantially decreased compared with the LER of undefoliated tillers [91]. In grazing studies, defoliation is generally less severe in frequency and intensity than in the weekly defoliation sequence experiment previously reported in Figure 3. However, since grazing tends to preferentially remove young leaves and thus tends to leave older leaves or older leaf portions, which have a lower photosynthesis rate, the lower proportion of leaf removal occurring in the grazing experiment was probably counterbalanced by a lower photosynthetic activity of the remaining leaf segments. Thus, besides the understanding of basic physiological processes that take place following a single defoliation, it is crucial to also consider their limits and to explore various defoliation sequences.

In addition to the potential effect of defoliation on leaf elongation, in relation to carbon and nitrogen supply and mobilization, defoliation may also reduce leaf elongation by damaging part of the intercalary leaf meristem. This frequently occurs in dicots, where more meristems are located at height above ground level, and therefore are directly susceptible to suppression. Although temperate grasses are generally considered as plants adapted to grazing [14], a recent study comparing several grass species has shown significant differences in leaf meristem tolerance to defoliation [92,93]. Under severe defoliation, *Dactylis glomerata* was better able to shorten the leaf growth zone and to compensate for its shorter meristem by a higher relative growth rate of its leaf growth zone compared with *Festuca arundinacea* and *Festuca rubra*, while *Lolium perenne* had an intermediate behavior. These data are in line with other observations that *Dactylis glomerata* is more tolerant to severe defoliation than *Festuca* species [94].

Independent of carbon supply and mobilization, the effect of light quality on LER is also significant. A decreased R/FR ratio led to higher LER in several C_3 and C_4 grasses [95]. In localized illumination experiments, the response of LER was significant when the emerged portion of the growing leaf was exposed to FR [96]. Blue light decreased LER in *Lolium perenne* [97]. More recent experiments [55] have confirmed this response and have shown that blue light may reduce LER to a much larger extent than previously shown in [97]. The negative effect of blue light on LER probably explains the negative effect of visible light on LER reported previously [68]. Therefore, several light signals develop during canopy development following defoliation (decrease in the R/FR ratio and a decrease in blue) and contribute to an increased leaf extension rate.

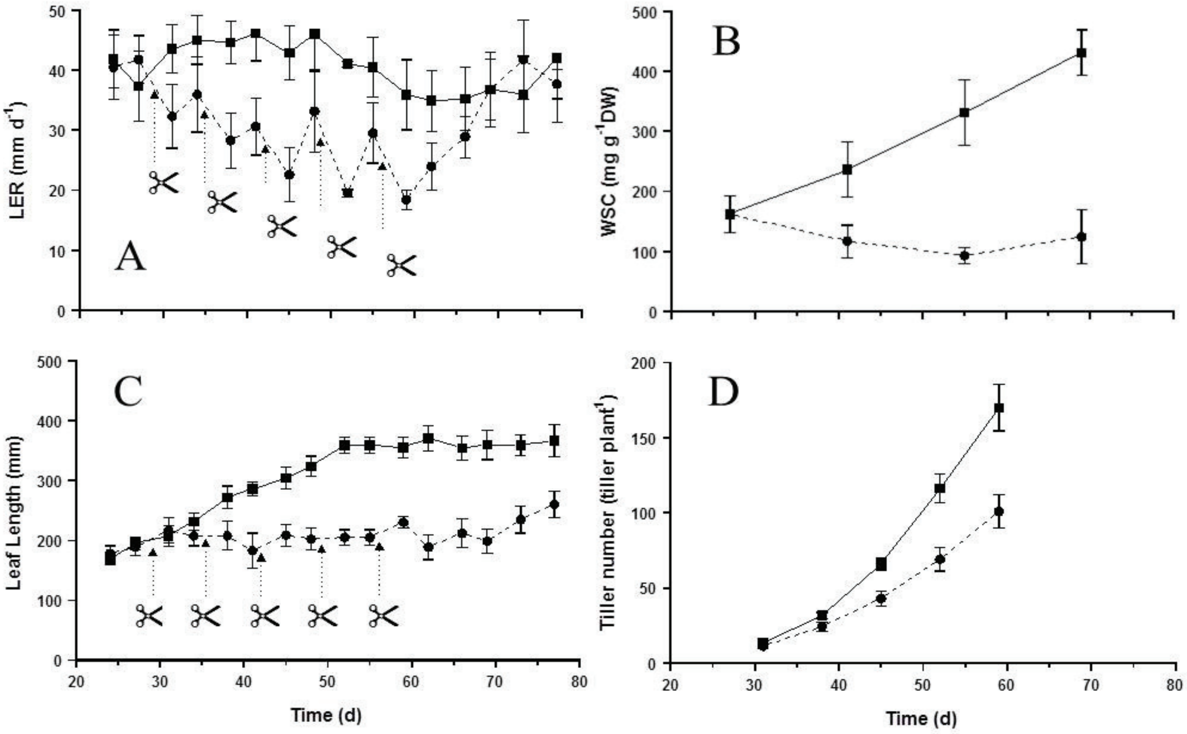

Figure 3. Effect of a sequence of 5 successive weekly defoliations (✂) applied to ryegrass plants, followed by a lax period allowing leaf growth recovery, on leaf elongation rate per tiller (LER, **A**),water-soluble carbohydrate concentration (WSC) in the leaf base (**B**), final leaf length (**C**) and tiller number per plant (**D**). ■ Undefoliated control plants; ● defoliated plants; d: day. Arrows indicate timing of the successive defoliations. Plants were grown under constant controlled conditions. Defoliated plants were clipped at a 5-cm stubble height [98].

3.3. Consequences of Defoliation on Leaf Length

During the ontogenic development of an undefoliated and isolated plant, successive leaves show a regular pattern of increase in final leaf length [47,56,61] (Figure 2A). The leaf elongation rate slightly increases in the first 2 or 3 leaves of seedlings [56], but remains approximately stable for leaves of higher rank, provided nutrient limitation or self-shading does not occur as plants get larger [61,99]. In contrast, the elongation duration of leaves of increasing rank increases very significantly [61] (Figure 2B). Therefore, the ontogenic increase in the length of successive leaves during tiller development is basically related to an increase in leaf elongation duration rather than to an increase in LER.

This ontogenic increase in leaf length with leaf number on a tiller is modulated by light quality. Blue light decreases the rate of increase of the final leaf length on a tiller to a large extent [97,100] (Figure 4). Moreover, blue light decreases sheath length to a relatively larger extent than lamina length.

In contrast, FR or the R/FR ratio increases the rate of increase of the final leaf length with leaf number [96,100]. At the sward level, the implication is that as undefoliated or infrequently defoliated tillers develop, and as leaf area index increases, the ontogenic tiller development, together with the decrease in blue light and the decrease in the R/FR ratio, act simultaneously and accelerate the increase in the final length of new leaves, as shown by green shading experiments that associate changes in light quality and light intensity similarly to changes in light composition occurring within the canopy during sward development [101].

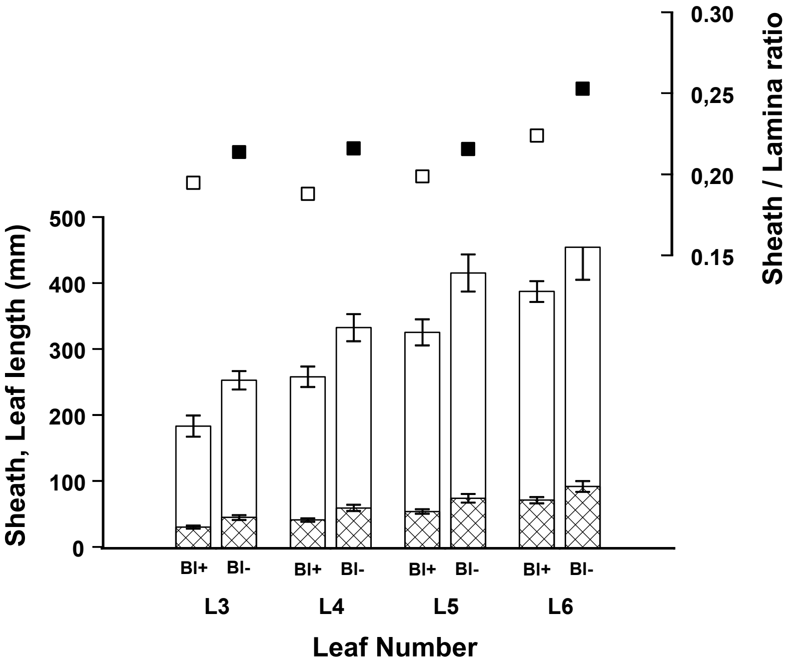

Figure 4. Effects of blue light on the final length of the sheath (hatched bar) and lamina (unfilled bar) of the four successive leaves of the main tiller of ryegrass (*Lolium perenne*). Light is provided by metallic iodure lamps (Blue+, □) or by sodium pressure lamps plus filters removing blue wavelengths (400–550 nm) and compensated to maintain a similar PAR (Blue−, ■). Adapted from [55].

Defoliation leads to a decrease in final leaf length in situations where leaves are cut below the ligule, but does not have a very significant effect when defoliation occurs above this point [47,48]. When significant, the negative effect of defoliation on final leaf length (Figure 3C) is simultaneously brought about by a decrease in the leaf elongation rate (see above for physiological determinants) and a decrease in leaf elongation duration. The physiological determinants are more obscure for LED than for LER. Several earlier studies have indicated that the sheath length of a mature leaf affects the final length of the following subtended leaf, and reduction in sheath tube length due to defoliation was the cause of the reduction in leaf length [47,64,102,103]. These studies suggest that the decrease in leaf length was associated with a decrease in LED. These results are confirmed by recent data showing a strong relationship between the length of the sheath tube from which a leaf emerges and the final length of this new leaf. This occurs similarly whether the source of variation in sheath length is the ontogenic increase in sheath length during development of an undefoliated tiller, whether it is the sheath length of axillary leaves and the leaves of its daughter tillers, or whether sheath length is reduced by defoliation (Figure 5). Therefore, there is good experimental evidence supporting the hypothesis that the length of the sheath tube also participates in the regulation of leaf length at the tiller level, in relation not only to its ontogenic development but also to defoliation intensity. It is currently unclear whether the impact of the sheath tube on the length of the following leaf is of the same physiological nature as the impact of blue light or R/FR, *i.e.*, whether the response to the sheath tube is determined by its effect on light quality perceived at the base of the growing leaf. Whatever the case, the fact remains that from a sward structure perspective, the influence of the sheath tube on leaf length operates in addition to the previously mentioned regulation of leaf length by light composition within the sward.

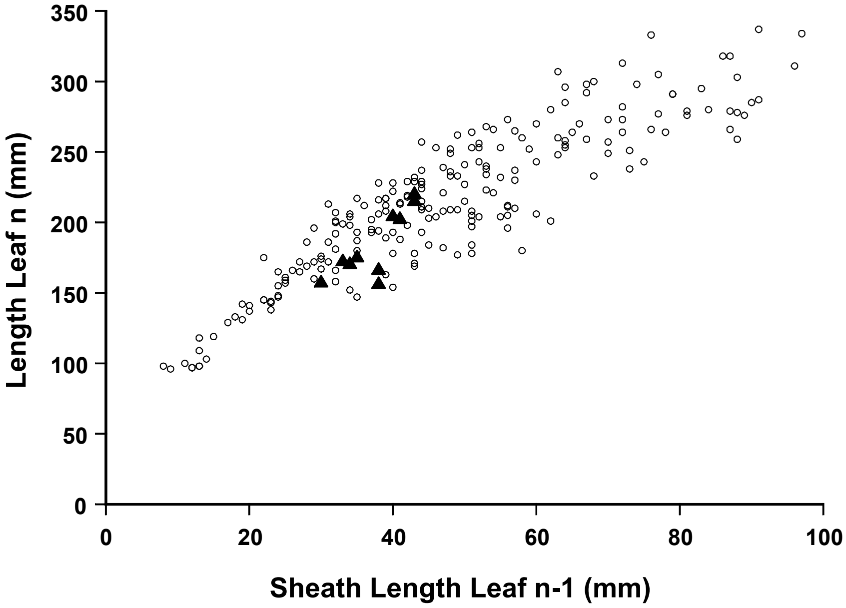

Figure 5. Relationship between the length of a tube sheath and the final length of the leaf that has emerged from the same tube on tillers (main and secondary tillers) of defoliated and undefoliated ryegrass (*Lolium perenne*). (○): undefoliated plants; (▲): weekly defoliated plants. The source of variation in sheath and leaf length is the ontogenic development (successive leaves on main and secondary tillers). Redrawn from [61].

As mentioned earlier, both LAR and LED appear to be correlated with sheath length. It can be emphasized here that a correlation between LAR and LED was also observed under conditions where sheath length was not the primary source of variation [99,104]. This relationship between LAR and LED is probably derived from the principle of growth co-ordination between successive leaves (*i.e.*, coordination of the successive phases of leaf development, from initiation to emergence and achievement of final size) as proposed in [105] or more recently in [106].

This principle of growth co-ordination between successive leaves also has other major implications. It explains the observation of a constant number of leaves growing simultaneously on a tiller [3,53]. It also explains that under undisturbed conditions of growth, the onset of leaf senescence (and consequently leaf life span) is coordinated with the development of newer leaves of a tiller, thus determining a constant number of mature living (green) leaves per tiller as observed in several pasture

C_3 grass species [3,53]. This has major implications (discussed in Section 4) with respect to herbage utilization.

3.4. Defoliation and Tillering

The appearance of new tillers occurs through the activation of axillary buds and the development of the first leaf primordium. Therefore, due to this physical link between the presence of a leaf and the presence of its subtending axillary bud (one axillary bud per leaf in many temperate grasses), tillering is limited by the number of leaves produced. Site filling [45,107] or site usage [58] indices have been used to evaluate the extent to which tillering rate is regulated by, or independently of, LAR. In addition to the physical link between leaf appearance and tillering, observations also show that the development of a tiller from an axillary bud is co-ordinated with the development of the subtending leaf, so that its probability of development is high at the end of cell division in the sheath of the subtending leaf [108], declines thereafter, and becomes low after two or three leaf initiation intervals on following phytomers [109]. Thus, the beginning of the development of a daughter tiller occurs within a narrow "window of opportunity", relative to the development of leaves on the mother tiller. This reinforces the link between the rate of appearance of leaves on a tiller and the rate of appearance of daughter tillers.

Basic principles of the regulation of tillering in swards may be illustrated in the simple case of the time trends of tiller density (the net balance between tiller birth and tiller death) in a regrowing sward following a single mechanical defoliation (Figure 6). In the first phase, soon after defoliation, tiller density rapidly and substantially increases (days 5–20, LAI below 4). In the second phase (days 25–30, LAI 4–6), the rate of increase in tiller density progressively decreases to zero, due to a very large decline, although not necessarily a complete cessation, of tiller appearance (data not shown). In the third phase (following day 35), tiller density decreases, mostly due to tiller death. As shown in [110], site filling is maximum under low LAI (phase 1 in Figure 6) and LAR is high, allowing a rapid emission of new tillers. As a sward develops and LAI increases, site filling decreases, indicating that high LAI down-regulates tillering *per se*, independently of any effect on LAR. In addition, since LAR also declines during plant ontogenesis (see Section 3.1) and sward development (Figure 6), the decline in tillering rate observed during the second phase is simultaneously determined by the decrease in LAR and by a decrease in site filling (or site usage). If site usage was limited by carbohydrate availability, the decrease in site filling would have happened in the first phase of sward development rather than in the second phase during which LAI is already restored to a large extent. There is now much evidence that tillering is regulated by light signals. Tillering is reduced under the low R/FR ratio that plants experience during sward development and at LAI values above 2–3 [49,96,111–115], mostly due to the increased delay between the appearance of a daughter tiller and the appearance of its subtending leaf. More recent data show that blue light does not play a significant regulatory role in site usage or LAR [55], and thus does not affect tillering. The absence of an effect of blue light on tillering contrasts with the large effect of the R/FR ratio.

Tiller death shown in the third phase of the above sward regrowth example is likely to occur due to the shading of young tillers that could not develop rapidly enough during sward development to maintain access to light and then C supply [3,116].

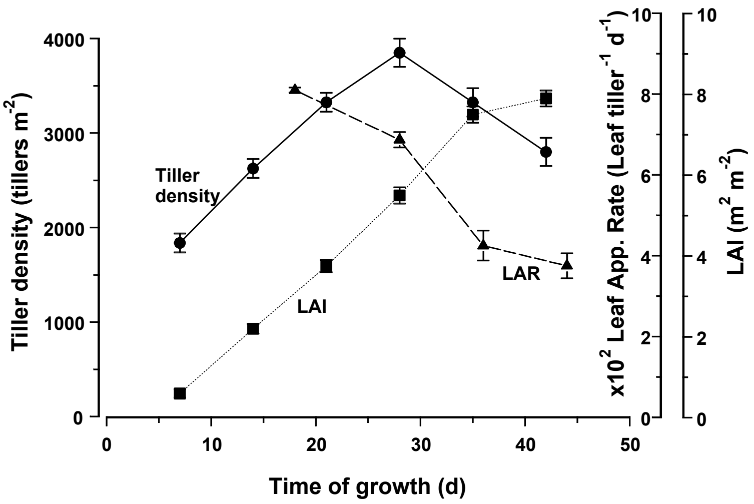

Figure 6. Time trends in tiller density (●), leaf area index (■, LAI), and leaf appearance rate (▲, LAR) for a tall fescue sward following a cut (at day 0). Adapted from [62].

A number of studies conducted on isolated plants show that tillering rate is reduced by defoliation, particularly when it is repeated and intense (Figure 3D; [46,47,49]). This decrease in tillering is probably due to a shortage of non-structural carbohydrates. Although the tillering rate is decreased by defoliation, it is not stopped even under frequent and intense defoliation (Figure 3D). Thus, under a sequence of repeated intense defoliation of isolated plants, the tiller number per plant continues to increase, while the leaf elongation rate progressively declines, leading to a major decrease in leaf length and therefore tiller size. This down-regulation of tillering by frequent and intense defoliation of single plants thus appears to be more limited than the large down-regulation that operates under high LAI in dense swards (during phases 2 and 3 in Figure 6). Therefore, the latter, determined simultaneously by the decrease in LAR and site filling as explained above, appears to be the basis of the size-density compensations observed at the sward level. Thus, although the impact of defoliation on leaf growth sometimes appears as a shorter-term response than morphological adaptations [17,18,84], from an ecophysiological point of view, they operate simultaneously and are part of an integrated plant-environment interplay. This probably explains why the adaptation of sward structure to defoliation, which allows the maintenance of sward productivity to a certain extent, is rapid and efficient.

4. Grazing Management, Herbage Production and Efficiency of Herbage Utilization

A grazed sward is a dynamic system where leaf tissues are continuously produced by tillers (growth, G) and are consumed by grazing animals (intake, I) or are senescing (S). Optimizing the quantity of herbage utilized by the grazing animal (I) requires two considerations: (i) maintaining a high rate of green herbage accumulation (G) and (ii) maximizing the efficiency of herbage utilization I/G, or equivalently minimizing herbage losses by senescence S/G. In continuous grazing systems, this highlights the conflict between maximizing G (by maintaining a high LAI) and minimizing senescence S (by maintaining a low LAI). Herbage growth increases asymptotically with sward LAI, in keeping with the quantity of intercepted radiation, while senescence increases linearly. Thus, under continuous grazing management, a compromise between herbage production and the efficiency of herbage utilization has to be found to maximize the amount of herbage intake. This optimum for pastures dominated by perennial plants in temperate regions is reached for swards maintained at LAIs of approximately 2–4 [117,118]. Under intermittent defoliation management (rotational grazing or cutting regime), the optimization of harvested herbage yield for the succession of regrowth periods requires that herbage be harvested when the maximum average growth rate is reached (Figure 1.8 in [18]). The time elapsing from the start of regrowth to optimum harvest depends greatly on the initial (or residual) LAI. The higher the initial LAI, the shorter the interval to optimum harvest [13].

In [13], a model was used to compare the relationship between average growth rate and average sward LAI under continuous and rotational sward management. It was demonstrated that the two managements are essentially part of the same continuum growth response to the average sward LAI. Thus, the key sward parameter that governs herbage production is the average LAI at which the sward is maintained. This average LAI can be maintained as constant as possible during a period under continuous stocking, or can vary from a low to a high value during the regrowth period in an intermittently defoliated system.

The efficiency of herbage utilization in a grazing system can be defined as the proportion of the gross leaf tissue production that is removed by the animals before entering the senescence state [18,28]. The calculation of the herbage utilization efficiency should consider the maintenance of a sward state that ensures the "sustainability" of herbage production, *i.e.*, that allows a more or less constant light interception by the sward. Under continuous stocking conditions, this situation corresponds to swards maintained at constant LAI or sward height [117]. For rotational grazing systems, this state corresponds to an average LAI at which the different paddocks are maintained over time [13]. The analysis of leaf tissue flux dynamics in grazed swards allows for the estimation of herbage utilization efficiency (HUE) as the proportion of the gross leaf tissue production (G) that is consumed by grazing animals (I). As demonstrated in [27] under continuous grazing conditions, the proportion of leaf length that escapes defoliation and then senesces can be estimated by the ratio between leaf lifespan and the defoliation interval. This ratio determines the average number of times an individual leaf can be defoliated before senescence [28]. For example, for an average leaf life span of 40 days and a defoliation interval of 20 days, each leaf should be defoliated 2 times before senescence. Given that the proportion of leaf length removed at each defoliation is relatively constant and averages 50% [27], it is possible to calculate the proportion of length of each leaf removed by animals. For an average leaf lifespan of about 40 days for tall fescue and an average interval of defoliation of 20 days, a theoretical herbage defoliation efficiency of 75% of leaf length can be predicted (Figure 1.7 in [18]). The defoliation interval decreases linearly with an increase in stocking density [6]. Therefore, when stocking density is increased under continuous grazing management, as a consequence of a higher herbage growth for maintaining a constant sward height (or LAI), then the leaf defoliation interval decreases, and for a given leaf life span, a greater proportion of leaf length is consumed by grazing animals, leading to an increase in herbage utilization efficiency. In particular, when herbage growth is stimulated by N supply, the increase in stocking density and the decrease in the leaf defoliation interval lead to a substantial increase in herbage use efficiency (Table 1).

Table 1. Comparison of herbage growth and herbage use efficiency of two tall fescue swards maintained at similar LAI in a continuous stocked system and receiving either a non-limiting N supply (N2) or a deficient N supply (N1). After [27].

	Herbage Growth Rate ($kg{\cdot}OM{\cdot}ha^{-1}{\cdot}day^{-1}$)	**Stocking Density ($Sheep{\cdot}ha^{-1}$)**	**Defoliation Interval (Days)**	**Herbage Use Efficiency (%)**
N1	56	28	28.4	57
N2	76	36	20.5	73

OM, organic matter.

Similar results have been obtained in natural pastures in the Pampa (Argentina) for several species where HUE increased from 50% to 67% after a supply of 100 Kg N in spring [29,119]. Thus it is possible to generalize these results and to conclude that in continuously grazed swards maintained at constant LAI, any increase in leaf tissue production, whatever the cause (temperature, nutrient or water supply, genetics) will lead to a further increase in stocking density, and accordingly to an increase in herbage use efficiency [28]. The magnitude of such an effect should be dependent on the leaf life span of the grass species in the sward. Species with a short leaf life span should be more responsible for a decrease in stocking density than species with a longer leaf life span. As a consequence, maximizing herbage use efficiency by using a high frequency of defoliation for a given leaf life span leads to a decrease in leaf litter production [16,118], thus reducing the return of C to soil. This illustrates the conflict between optimizing herbage harvested by grazing animals and accumulation of soil C, as demonstrated in [120].

In intermittently grazed swards, the leaf defoliation interval is highly disconnected from stocking density and herbage growth. The interval of defoliation is determined by the frequency of moving animals from paddock to paddock and depends mainly on farmer decisions based on animal number, paddock size and paddock number. In such a system, the instantaneous stocking density is high enough for the great majority of tillers to be defoliated several times within a short time interval of a few days. Therefore, the efficiency of herbage utilization will be determined by grazing pressure, *i.e.*, the quantity of leaf tissues offered per animal and per day. The interval of defoliation is then determined by the rest period (number of days between two successive grazing events). If the rest period remains shorter than the average leaf lifespan of the grass species considered, then the efficiency of herbage utilization will be optimized, but if the rest period becomes longer than the leaf life span, or/and to a lesser extent if the residual herbage mass after grazing is increased, then a greater proportion of leaf tissue situated within the sward horizon accessible to animals will die before the next grazing period, and the efficiency of herbage utilization will decline.

When intermittent and continuous gazing systems are compared, similar quantities of herbage intake and similar herbage utilization efficiency are obtained when the conditions for herbage growth are favorable (spring period, high level of N supply and no water deficit; [13]), and animal performance is roughly equivalent. But when herbage growth becomes limited by environmental conditions, the herbage use efficiency of continuously grazed swards declines as a result of the associated decline in stocking density and then defoliation frequency (as explained previously), while this relationship between stocking density and defoliation frequency can be disrupted in rotational grazing through the adoption by the farmer of an adequate rest period for maintaining the defoliation interval as constant as possible relative to the leaf life span of the dominant species. Thus, in extensive grazing systems, the use of an intermittent grazing system should be more efficient than continuously stocked ones.

5. Conclusions

Although it has been recognized from the beginning of the 1970s–1980s that swards are able to adapt their structure to defoliation, particularly in terms of tiller size and tiller density, thus allowing maintenance of productivity to a certain extent within a range of LAI, the underlying ecophysiological mechanisms were largely unclear. The present review shows that since then, our understanding of these mechanisms has progressed to a large extent, at least for several grass species. The involvement of a large number of regulating factors related to plant physiology (N and C reserves, plant morphology, structure of meristems) as well as environment (light signals) is highlighted. The contribution from responses of multiple plant morphogenetic components is also demonstrated. This complexity of regulating factors and plant morphological responses necessitates the development of an integrated comprehensive approach. Modeling methodologies have been developped during recent years. Several descriptive morphological models have been proposed [29,84,119,121,122]. Additionally, several structure-function virtual modeling approaches have been proposed more recently [106,123–127]. These modeling approaches are valuable tools to integrate current knowledge and improve our understanding of the complex nature of the regulation mechanisms involved.

Most of the present review reports data available for temperate grasses. Very similar information on the role of C and N reserves is also available for lucerne and white clover. Responses to light signals have also been described for white clover [36,124,128–130]. However the role of light signals is almost undescribed in other dicots. Therefore, dicot species deserve particular attention in future research.

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Author Contributions

François Gastal is the main contributor for Sections 1–3 and 5 of this review paper. Gilles Lemaire is the main contributor for Section 4.

Conflicts of Interest

The authors declare no conflict of interest.

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