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Tillering Regulation by Endogenous and Environmental Factors and its Agricultural Management

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ABSTRACT

The outgrowth of axillary buds in grasses, known as 'tillering', has been extensively studied over many decades because of its agronomic importance and biological interest as well. The control of tillering has proven to be multi-factorial and very complex. The physiological complexity of this process is demonstrated by the wide array of environmental, endogenous and biotic effects that, together with their interactions have been shown to modulate tillering. In this review we analyze current knowledge about the tillering process at both isolated plant and canopy levels, and discuss the opportunities for integrating experimental results into a unifying theory that can account for all effects and thus overcome the shortcomings of the previously proposed nutritional and hormonal hypotheses. We discuss recent advances on the control of tiller development by endogenous, environmental and biotic factors at the isolated plant level, while the empirical rules that had been developed to allow proper tiller management at a canopy level are presented in connection with available physiological basis. Attention is also given to the recent development of simulation models that provide a powerful tool for agronomic management of tiller dynamics, which in turn may facilitate, through their validation, new insights on the control of tillering by the plant.

Keywords: apical dominance, axillary buds, grass

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INTRODUCTION

The process of outgrowth of axillary buds in grasses is known as 'tillering'. Because of its agronomic importance for grain and forage productions, turfgrass, or even for ornamental purposes, tillering has been extensively studied over many decades. The control of tillering in grasses has proven to be multi-factorial and very complex, and although recent research has provided insight into the contribution of many genetic and physiological factors and their interactions with the environment, there is still need for a unifying theoretical synthesis of known effects.

A grass plant can be considered as a collection of tillers that arise from a single primary tiller or crown (Skinner and Nelson 1992). In annual grasses tillers are produced at a specific stage of their life cycle (*i.e.*, the tillering stage) while in perennial grasses tillering is an ongoing process that takes place along the plant lifespan. Consequently, a single plant may represent several generations of tillers (Moore and Moser 1995). As each grass stem develops, new tillers usually appear from the leaf axil just below the youngest fully expanded leaf (Skinner and Nelson 1992). Hence, the rate of leaf appearance determines the maximum tiller appearance rate. Tillering activity may be quantified in terms of site filling, F_S, first defined by Davies and Thomas (1983) as the rate of production of tillers in relation to the rate of leaf appearance. This is equivalent to the natural logarithm of the factor by which tiller number per plant increases with each leaf appearance interval in the mainstem (Bahmani *et al.* 2000). Site filling has a theoretical maximum of 0.6931 ($\mathrm{Log}_n 2$), which corresponds to doubling of tiller number with each leaf appearance interval (Neuteboom and Lantinga 1989). Other measures have also been proposed, i.e., site usage which takes account of the proportion of available buds used along a length of stem (Skinner and Nelson 1992); and nodal probability (Matthew *et al.* 1998) or specific site usage that take account of the fraction of buds that ultimately develop into a visible tiller at a specific site (Bos and Neuteboon 1998) with a maximum of 1 or 100% (Matthew *et al.* 2000). A maximally-tillering plant is illustrated in **Fig. 1**.

Unfortunately, not all studies on tillering give measure-

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Invited Review

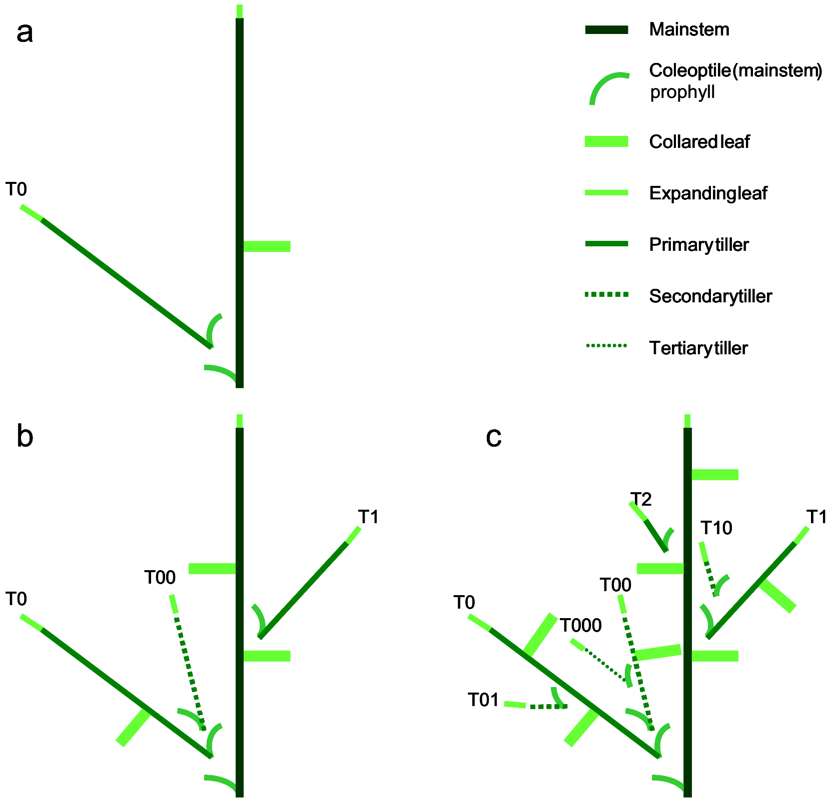

Fig. 1 Potential tiller production pattern for one (a), two (b) and three (c) fully emerged leaves with the ligule expose (collared leaves) on the mainstem (adapted from Skinner and Nelson 1992 and Bos and Neuteboom 1998). Potential tiller number can be estimated as $T_{max} = 2^{CL}$ where T_{max} is the potential number of cumulative total tillers per plant (including mainstem), CL is the number of collared leaves.

ments of leaf number on the main axis, so it is sometimes difficult to ascertain whether a given treatment causes a change in tiller number as a consequence of increased site filling, a more advanced plant development, or both. In this review we will mainly refer to changes in tillering when it is apparent that the effects are at least in part the consequence of changes in site filling, even when this is not explicit in the original source.

The tendency to develop tillers widely differs among grasses. Two main forms of grass vegetative architecture are encountered: the Pooid and Erhartoid cereals such as wheat (*Tritricum aestivum* L.) and rice (*Oryza sativa* L.) have multiple basal tillers on the mainstem, while Panicoid cereals such as maize (*Zea mays* L.), sorghum (*Sorghum bicolor* (L.) Moench) and the millets have few tillers or even only a single mainstem. These differences are starting to be analyzed by means of a combination of phylogenetic and genomic analysis, but must be also viewed in both an evolutionary and ecological framework (Doust 2007). In the latter sense, tillering may be considered as a strategy to occupy space close to the mother plant (even though a certain movement can actually occur on a horizontal plane because of oblique growth of the tiller; see Lafarge 2001). This strategy is sometimes called a ‘phalanx strategy’, as opposed to a ‘guerrilla strategy’ exhibited by plants that develop rhizomes or stolons and thus may explore rather distant sites (Lovett Doust 1981).

Tillering confers environmental plasticity to grain crops such as wheat and many other winter cereals. Plants that are able to develop tillers can compensate for low sowing densities or seedling losses during early crop stages, and usually without much variation in maturity time when low seeding density results in more heads being formed through tillering from mainstems (Hay and Kirby 1991). This compensation ability allows for stable yields per unit soil area among a certain range of sowing densities. On the other hand, there exists a ‘critical’ tiller density above which no further increases in yield occur (Holliday 1960).

Environmental plasticity is also important in the case of forage grasses. In perennial pastures, a high tiller production capacity improves chances of persistence after periods with unfavourable environmental conditions, during which plants may experience biotic and abiotic stresses leading to the death of parts of the plant. Tiller production is a key factor involved in the resistance of grasslands to deterioration by ageing (Lafarge and Loiseau 2002). This is because when a tiller dies as a consequence of flowering, apex removal (by grazing or cutting) or apex destruction (by trampling or burning), it has to replaced it in order to sustain forage production in the longer term (Bartholomew 2009).

In the case of turfgrass for recreational purposes, it may be necessary to obtain high tiller densities for smooth ball rolling, which also tends to confer resistance to weed establishment (Cattani and Struik 2001).

Early physiological studies on tillering were based either on the supply and/or deprivation of putative growth regulators (hormones, sugars or mineral nutrients) or on the modification of the environment (light quality, light intensity or photoperiod), and a wealth of information has been gathered, mainly comprising correlative evidence. However, the precise role of all these factors is still a matter of discussion, because of complex interactions that make generalizations very difficult. Anyway, empirical rules have been developed that allow proper tiller management at a canopy level in swards, but few studies have dealt with the physiological basis of these rules.

In this review we will analyze current knowledge about the tillering process at both isolated plant and canopy levels, and discuss the opportunities for integrating experimental results involving a wide array of factors that affect tillering within a unifying theory that can account for all effects.

CONTROL OF TILLERING IN ISOLATED PLANTS

Traditionally, factors affecting tillering have been divided in two major groups ‘Endogenous factors’ and ‘Environmental factors’ for study purposes (i.e., McSteen 2009). Nevertheless, it must be born in mind that actually both kind of effectors are not independent; on the contrary, they frequently interact. For instance, light (environmental factor) increases assimilate availability (endogenous factor) favouring root development, and thus, cytokinin production (another endogenous factor) which in turn increases plant development affecting the light environment. A third major factor has been included in the present review, namely the 'Biotic factor', which deals with interactions with microorganisms whose effects on tillering have deserved increased attention lately.

Endogenous factors

1. Ontogenic control of tillering

In grass shoots, not all axillary buds develop into tillers, but many of them remain dormant or even die during plant ontogeny. It has been proposed that, in temperate forage grasses, the outgrowth of the axillary bud is coordinated with other events that take place almost simultaneously on the main axis (Nelson 2000). Skinner and Nelson (1994) have proposed that this synchronization involves at least three adjacent nodes: 1) at the oldest node, cessation of cell division in the leaf sheath would be accompanied by initiation of cell division and elongation in the associated tiller bud; 2) at the next younger node the ligule would be initiated; and 3) at the youngest node cell division would start in the primordium of the leaf while elongation of a new leaf blade would begin. These researchers have suggested that, because of this synchronization of events, the cell division process would play a key role in regulating leaf and tiller development. The mode of action of this synchronic process has been further analyzed in the work of Fournier *et al.* (2005). Although in general, the highest probability for an axillary bud to be released occurs when cell division in the sheath at the same node stops, under certain circumstances, for example following defoliation, the outgrowth of an old axillary bud can take place (Nelson 2000).

For an axillary bud to end dormancy and develop a new tiller, a large number of molecular and biochemical changes must take place. The discovery of cyclins, proteins that control the progression of cell cycle by regulation of cyclin-dependent kinases and that are synthesized or degraded as needed to drive the cell through the different stages, opened a whole new area in biology, and abundant information about molecular steps of this process is now available (Mironov *et al.* 1999).

Classic genetic analysis has led to the conclusion that tiller number is usually controlled by quantitative trait loci (QTLs) which act mainly by additive, rather than epistatic or dominant, effects (Tang *et al.* 2001). For instance, working with a doubled-haploid rice population of 123 lines, Yan *et al.* (1998) reported that the number of QTLs significantly affecting tiller number was different at different plant stages, and that many QTLs controlling tiller growth identified at early stages were undetectable at the final stage, while only one QTL could be detected across the whole growth period.

However, modern molecular analysis is needed to provide a more direct evidence of the processes involved. A number of genes have been identified in relation to tiller initiation and outgrowth. (Beveridge *et al.* 2007). Although by themselves these studies cannot be sufficient for understanding the physiological basis of tillering, they provide useful insights about the processes that occur when an axillary meristem ends dormancy to originate a branch. The following section aims to revisit the information obtained by classic approaches providing an interpretation in the light of modern biochemical and molecular findings.

The tillering process in grasses is obviously analogous to release of apical dominance in dicotyledons, and much of the information gathered is a consequence of the replication in grasses of studies performed in dicots. Moreover, modern genetic techniques have revealed that many pathways of tillering control are conserved between monocots and dicots (e.g., Johnson *et al.* 2006; Zou *et al.* 2006). However, this association is sometimes overemphasized, and differences between plant classes minimized. For instance, some recent studies on hormonal control of bud activity in general (i.e., Beveridge *et al.* 2007) or on tiller formation in particular (Tomlinson and O'Connor 2004; McSteen 2009), deal almost exclusively with auxin and cytokinins, the hormones that have proven to exert a decisive role in branching in broad leaved plants. The role of these hormones in the modulation of tillering of grasses by the environment is however not so clear, and there is good evidence of the participation of other hormones (i.e., gibberellins and ethylene) that are not mentioned in these studies. Current knowledge about the role of plant hormones and other signalling molecules on tiller bud outgrowth will be reviewed below.

2. Plant hormones

Auxins - Cytokinins. The involvement of auxins in the control of tillering was originally proposed by Leopold (1949), who pioneered the application of the apical dominance hypothesis, originally developed for dicots, to a grass (barley). This hypothesis (also called the 'hormonal hypothesis') indicates that indole-3-acetic acid (IAA) produced in the apical meristem (and young leaves), directly inhibits axillary bud growth. However, it was abandoned later (during the 1950s) because of experimental and interpretive inconsistencies and the demonstrated involvement of a second hormone, cytokinin, in apical dominance. The cytokinin deficiency hypothesis replaced the direct hypothesis as the current hormonally based interpretation of apical dominance, which then stated that IAA produced in the apical meristem would block the synthesis or utilization of cytokinin within axillary buds, thus inhibiting their growth.

However, as pointed out by Murphy and Briske (1992), there are many inconsistencies with this reformulation, one of them being the fact that apical meristem removal does not always promote tiller initiation in grasses and tillering may occur in plants with intact apical meristems. Experiments with the addition of auxin inhibitors failed to elicit the expected response (Jewiss 1972). On the other hand, variable results have been encountered when studying the effects of cytokinins, and while both the experiments of cytokinin injection to wheat buds by Jewiss (1972) or correlative evidences of endogenous cytokinin content and tillering in Agrostis (Wang *et al.* 2004) support the participation of this hormone, the work of Woodward and Marshall (1988) with exogenous application of cytokinins to barley leaves, or the study of Pérez *et al.* (2006) with cytokinin supply to the root medium fail to support it. The statement by Murphy and Briske (1992) that despite wide acceptance, the interpretive value of the apical dominance concept regarding tillering is much less consistent than generally assumed, and that it may be an incomplete and restrictive interpretation of the regulation of tiller initiation in perennial grasses, is still valid. Hence, recent work has attempted to include the participation of additional factors, either endogenous (Beveridge 2006) or environmental (Tomlinson and O'Connor 2004). Evidence supporting the participation of these additional factors is discussed below.

Carotenoids. A further reformulation to the apical dominance hypothesis was needed when it was discovered that a compound that is derived from carotenoids, called strigolactone, may alter the auxin/cytokinin control of tillering (Ferguson and Beveridge 2009; Stirnberg *et al.* 2010). Strigolactone, which is known for its triggering effect of germination of parasitic plant seeds and for stimulating symbiotic fungi, appears to correspond to the originally described SMS (shoot-multiplicational signal), a root hormonal signal that inhibits shoot branching in plants and which had escaped earlier identification (Gómez Roldán *et al.* 2008). The discovery of SMS occurred about a decade ago when hormone analysis and grafting studies of the *ramosus1* (*rms1*) branching mutant of garden pea (*Pisum sativum*) showed that a long-distance signal other than cytokinin or auxin was responsible for the branching phenotype of this mutant (Beveridge *et al.* 1997; Foo *et al.* 2001). Several genes in the SMS pathway have now been cloned in Arabidopsis, pea and petunia (*Petunia hybrida*), and a picture of how cytokinin, auxin and SMS regulate shoot branching in these species is emerging (Beveridge 2006).

Nevertheless, as Dun *et al.* (2006) have stated, available evidence does indicate that these hormones (auxins, cytokinins, SMS) act at a transition stage to induce the progression to sustained growth. Research is needed to identify when and where buds are in a transition stage, since some observations may be the product of consequential, rather than causal, events in bud outgrowth, because of feedback processes that result from, rather than induce, particular stages of bud outgrowth.

Ethylene. Tillering and tiller growth has been shown to be stimulated by ethylene in oat according to Harrison and Kaufman (1982). More recent experiments support this finding (Rajala and Peltonen-Sainio 2001). It is interesting that in wheat hydroponic culture, lack of aeration causes enhanced tillering (Pérez *et al.* 2006), which may be associated with the fact that in flooded root media, ethylene concentration increases in plant tissue both due to enhanced synthesis as well as entrapment. In agreement with these findings, a trend for a higher tiller production in flooded than in nonflooded soils has been reported for rice by Yan *et al.* (2010). Rajala and Peltonen-Sainio (2001) have proposed that tillering promotion by ethylene might be the consequence of ethylene-mediated inhibition of auxin biosynthesis and movement (Morgan and Gausman 1966; Lyon 1970; Evans 1984).

Gibberellins. The possible participation of gibberellins in the tillering process received early attention. While results of gibberellin application have sometimes been contradictory (Langer 1963), in general, it can be concluded that gibberellins tend to cause less development of axillary buds, and also to promote the elongation of already initiated stems (including tillers) (Jewiss 1972; Rajala and Peltonen-Sainio 2001). On the other hand, there is quite clear evidence indicating that the application of gibberellin inhibitors promotes tiller initiation, in parallel with stunting of the main axis of the plant (Lee *et al.* 1998). Interestingly, these authors found that the pre-GA12 biosynthesis inhibitors CCC, uniconazol, and ancymidol all reduced height and promoted tillering while, in contrast, inhibitors of the GA20 to GA1 step, CGA and BX-112, also inhibited height growth but failed to promote tillering. This suggests the existence of separate gibberellin-mediated pathways controlling tillering and plant height. In recent work from our laboratory, the application of a different GA-inhibitor, paclobutrazol, led to axillary bud development in wheat plants cultivated under non-inductive environmental conditions (low light intensities and warm temperatures), under which no tillering at all was observed in control plants (Pérez 2007).

Many rice mutants have been described that lack, or are insensitive to, gibberellins; and an association between dwarfism and high tillering in rice has been reported in many studies (i.e., see Ishikawa *et al.* 2005). However, it must be pointed out that lack of gibberellins (or insensitivity to this hormone) seems not always to be the cause of dwarfism (Zou *et al.* 2005). Nevertheless, direct evidence of the involvement of gibberellins in tillering was provided by Frantz *et al.* (2004), who described a 'Super Dwarf' gibberellic acid–deficient rice which is only 30 cm tall, and produced about 50 tillers per plant. In the opinion of these authors, Super Dwarf rice excessive tillering may be due to the lack of apical dominance caused by a lack of active GA.

The inverse association between tillering and leaf elongation also has been found in a number of grass species other than rice; the possible involvement of GAs, which are usually associated with leaf elongation in grasses, remains to be studied. For example, Gautier *et al.* (1999) studied the tillering responses to the light environment and to defoliation in two populations of perennial ryegrass (*Lolium perenne* L.) selected for contrasting leaf lengths and found that selection for longer leaves reduced the tillering rate, and this difference between short- and long-leaved populations was magnified by defoliation and by decreasing the red: far red (R: FR) ratio. Similarly, Bahmani *et al.* (2000) found in this species that Grasslands Ruanui (a short leaved ryegrass cultivar) had a higher tiller number per plant than Ellett (long-leaved) irrespective of light environments, and that this response could be explained by higher site filling, with similar leaf appearance rates. In this work the higher tillering variety had lower leaf elongation rate, so intraplant competition for C-substrate might be implicated. No attempts to measure gibberellin concentration or sensitivity to this hormone were made in these studies.

3. Assimilate availability

One of the traditional hypotheses (the 'nutritional hypothesis') proposed to explain tillering control states that axillary bud development is dependent upon supply of photoassimilates. It is clear that available assimilates may be invested in the outgrowth of tillers before newly expanded leaves can fixate carbon so as to compensate for this early investment. Nevertheless, the most suggestive evidence for such a role of assimilates is the fact that tiller promotion is almost always associated with environmental conditions that favour carbon fixation over carbon use, namely: high light intensity, high R: FR ratio, low temperature, and high nitrogen availability.

Modern studies have focused on sugar signalling of plant metabolism, and the fact that sucrose may act as a signalling molecule that elicits several physiological processes is now supported by a good bulge of evidence (Farrar *et al.* 2000). For instance, sucrose initiates a signalling pathway that leads to the induction of fructan metabolism in wheat and other winter grasses, in a process that requires the participation of calcium and protein phosphorylation and dephosphorylation (Martínez Noël *et al.* 2001, 2006, 2009). In nature, fructan metabolism is induced under the same environmental conditions that tillering is (i.e., high light intensity and low temperature).

Experiments with the addition of sucrose have on many occasions given rise to morphological responses in plants, such as enhanced root development in soybean and other dicots (Abdin *et al.* 1998; Begna *et al.* 2002). Particularly in grasses, Montaldi and coworkers pioneered studies on morphogenetic effects of sucrose after finding that the addition of this sugar changed the growth habit of *Dactylis* and other related species, from erect to prostrate (Montaldi 1970; Willmoes *et al.* 1988).

Other evidences supporting the nutritional hypothesis include work by Lauer and Simmons (1985) who found that young barley tillers imported photoassimilates preferentially from the subtending leaf on the main culm and from the leaf immediately above, while removing either the subtending leaf or the leaf above drastically reduced tiller emergence. On the other hand, Deregibus *et al.* (1985) pointed out that the inhibitory effect on tiller development of low R : FR ratios was not associated with reductions in photoassimilate levels.

Direct involvement of sucrose on tiller bud outgrowth has not been demonstrated to date. Several decades ago, Jewiss (1972) reported that the addition of 2% sucrose in axillary buds of wheat leaves had no effect at all on the subsequent fate of these buds. Also, in a recent work at our laboratory, the addition of sucrose to the root medium in varying concentrations to hydroponically grown wheat had no promotive effect on tillering (Pérez *et al.* 2006).

The 'nutritional hypothesis' is still frequently cited for explaining tiller outgrowth (i.e., Lafarge *et al.* 2002; Luquet *et al.* 2006). On some occasions, it has been combined with that of hormonal signals ('combined hypothesis'), as in the relatively recent reformulation by Tomlinson and O'Connor (2004). But, despite this volume of information and speculation, the case for the so–called 'nutritional hypothesis' is still not conclusive, and the association between tillering and assimilate availability appears to still be mostly correlative and not necessarily indicative of a cause–effect relationship.

Environmental factors

1. Light

Light intensity. There is wide evidence indicating that increasing light intensity on canopies leads to higher tillering in grasses (Evans *et al.* 1964; Friend 1965). This effect is more important than that of light on leaf appearance rate, as can be observed in the study of Mitchell (1953) on ryegrass. Hence, higher light intensities lead to higher site filling values, as also reported by Bos and Neuteboom (1998) for winter wheat.

Importantly, Mitchell and Coles (1955) found that this promotive effect occurs when the whole plant, rather than its base, received the increased intensity. Therefore, it would appear possible that the light intensity tillering promotion occurs *via* an increased photoassimilate production. Alternatively, since increased carbon availability usually leads to enhanced root growth and proliferation, tillering might be promoted because of more cytokinins transported from roots. Nevertheless, the induction of new roots by new tillers makes it sometimes difficult to ascertain whether this new root growth is the source of changes in tillering rate or rather is an effect of tillering itself.

The effects of light intensity on tillering may be mediated by changes in assimilate availability, but light intensity is also known to modulate plant development by at least another two pathways, namely the high irradiance response, and the redox signalling pathway (Oswald *et al.* 2001; Foyer and Noctor 2005; Walters 2005). The high irradiance response has traditionally accounted for several physiological responses such as stomatal opening, photoperiodic flowering and stem growth modulation among other features of vegetative development. This response has been mainly associated with red and blue photosensors, although recent evidence suggests that green light may also be involved (Folta and Maruhnich 2007). On the other hand, the redox signalling pathway is associated with excessive reduction of photosystem II due to surplus light capture, and is supposed to modulate plant growth habit including leaf and internode length (Huner *et al.* 1998; Ensminger *et al.* 2006). To our knowledge, the possibility that light intensity may modulate tillering through these two light signalling pathways has not yet been addressed.

Light quality. The involvement of phytochrome in the release of axillary buds was first reported by Casal and coworkers (Casal *et al.* 1985; Deregibus *et al.* 1985; Casal *et al.* 1986; Ballaré *et al.* 1987; Casal 1988), who found that increasing the R: FR ratio of the light incident on the base of ryegrass plants led to increased tiller development. Similar results were reported by Kasperbahuer and Karlen (1986) in wheat. Tillering is so sensitive to light quality that it may be promoted even by the physical act of tagging tillers for research purposes because of allowing brief light ingress in the surrounding sward (Matthew *et al.* 1998).

Because the R: FR ratio tends to decrease when light passes through (or is reflected from) green leaves, tillering would be inhibited in dense canopies with tall plants. Under these conditions, plants not only reduce tillering (Wan and Sosebee 1998) but increase sheath length (Barnes and Bugbee 1991; Knauber and Banowetz 1992) as well, which is part of the etiolation syndrome (and seems to involve increased gibberellin levels, or sensitivity to this hormone; Cooke and Saunders 1975). This morphogenic response consumes photoassimilates, and reduces root growth as well. Therefore, it is uncertain whether phytochrome *per se* is the triggering signal of tillering control, or if it exerts its role through changes in gibberellins, assimilate availability, or cytokinin production. Clearly, more research is needed to elucidate this question.

Photoperiod. Several studies have dealt with the role of photoperiod in tillering. In general, responses appear to differ between species and even between genotypes within a species (Lafarge 2000; Miralles and Richards 2000). However, it also appears that, within a genotype, photoperiod may influence tiller bud outgrowth in an opposite manner to the effect on floral bud initiation; i.e. in *Poa pratensis*, which flowers under long photoperiods, short photoperiods would favour tillering (Aamlid 1992). According to Hay and Kirby (1991), promotive effects of photoperiod on tillering could be mainly attributed to the prolongation of the tillering stage rather than to enhancement of bud outgrowth. Photoperiod duration is known to alter cytokinin levels (Wang *et al.* 2004) so the possible association between photoperiod and tillering *via* cytokinin content deserves further study.

2. Temperature

Mean temperature. There are several pieces of evidence indicating that low temperatures promote tillering in grasses, when plants are compared at a given developmental stage. One illustration of this is given by the comprehensive work of Friend (1965). However, it must be taken into account that this is an effect on site filling and not on the number of tillers per plant at a given time, which may be reduced by low temperature due to slower leaf development on the main axis (with consequential reduction of the maximum possible tiller number).

The effect of low temperature on tiller bud outgrowth illustrates the complexity of tillering control in grasses. Low temperature might exert its effect by changing many physiological variables that are, in turn, expected to have an effect on tillering.

Low temperatures favour assimilate availability, since under these conditions growth is more affected than carbon assimilation (Pollock 1990). Furthermore, differences between genotypes within a species are common: in wheat plants, concentration of sucrose and other sugars increases much more in winter than in spring types during periods at low temperature. This is related to the effect of cold on plant size: winter wheats are smaller than spring types (Equiza *et al.* 1997, 2001; Equiza and Tognetti 2001, 2002). Then, if assimilate concentration played an important role in tillering, both wheat types should tiller more at low temperature than at warm ones, and this effect would be more important in winter types than in spring ones. According to results from our laboratory (Lorenzo *et al.* 2007) this is only partially so: at low temperature, winter wheat varieties were found to tiller more than spring ones, but spring ones did not tiller more at cold, despite extensive accumulation of sucrose and other sugars, than at warm temperature.

This raises the possibility that the temperature effect might also be mediated by hormones, likely gibberellins. It has been reported that levels of this hormone fall in grasses during periods at low temperature (Pinthus *et al.* 1989). It is possible that gibberellin content in spring cultivars is higher than in winter ones, especially at low temperatures, which maximize size differences between cultivars. Further complications exist: at low temperatures, components of photosystem II are in a reduced state because of excessive light capture, and this in turn is expected to induce morphological changes leading to a compact growth habit (Huner *et al.* 1998).

In addition, the difference between day and night temperature (DIF) might affect tillering. Pinthus and Meiri (1979) reported that tillering and tiller development can be markedly promoted in different wheat cultivars by a low day/high night temperature regime. In their work, the elongation of leaf blades and stem internodes were strongly inhibited under this regime. These authors attributed such effects to changes in the endogenous hormone balance of the plants brought about by temperature; the hormones involved in the DIF response may be either gibberellins or auxins (Grindal *et al.* 1998; Thingnaes *et al.* 2003, respectively).

3. Water

Tillering is usually severely affected by low water availability. This is expected since leaf elongation is the first and most sensitive process altered by water deficits, and consequently, so is leaf appearance too. This in turn, decreases the number of potential sites for tillering. For example, Stark and Longley (1986) found that soil water deficits decreased the rate of appearance of mainstem tillers and also severely reduced development of tillers at the coleoptilar node. They also reported that in plants subjected to drought tillers appeared over longer intervals than in fully irrigated plants, and that when stressed plants were re-irrigated, the appearance rate of affected tillers frequently increased. The latter response is possibly mediated, at least in part, through a photomorphogenetic effect due to lower leaf area development, and consequently more favourable light conditions in the base of the plants. In some cases, this stimulation of tillering in re-irrigated plants was sufficient to compensate for earlier tiller losses. However, they also found that when the stress was extended into the latter part of the vegetative period, maximum tiller populations were reduced.

Similarly, working with *Triticum tauschii*, Cone *et al.* (1995) reported that not only was maximum tiller number strongly reduced by water deficit, but also initiation of tillering was inhibited until water was reapplied. These authors also noted that water deficit tended to increase the phyllochron.

However, the fact that water deficit has a profound effect on leaf appearance rate makes it difficult to ascertain whether reduced tillering in stressed plants is attributable to lower site filling or to delayed development. The work by Van Loo (1992) was directed to elucidating these possibilities. In this work, tillering and growth parameters of perennial ryegrass were determined in a glasshouse experiment using hydroponic culture at different water potentials. This author found that at low water potential (-1.3 MPa), final plant tiller number was 20% lower than in controls because of a reduction in the leaf appearance rate in the first weeks after the start of the stress treatment. On the other hand, site filling was only slightly affected by water potential. Thus, water availability seems not to exert a direct role upon tiller bud outgrowth, but rather an indirect one as discussed above.

4. Mineral nutrients

Nitrogen. A positive effect of N availability on tillering has been frequently found (McKenzie 1998; Cruz and Boval 2000). According to Lemaire and Chapman (1996), this effect is mainly attributable to changes in site filling since the leaf appearance rate depends only loosely on N nutrition levels in temperate grasses. The inductive effect of this nutrient on site filling may be associated to its well known effect on promoting cell division (MacAdam *et al.* 1989). The effects of N are not only evident when crops or swards are fertilised, but also in urine patches, at the time of urine deposition, in grazing pastures (Matthew *et al.* 1998).

The involvement of N availability in control of tillering has been discussed by Tomlinson and O'Connor (2004). These authors suggest that N has a strong mediatory role over tiller production through cytokinin production by roots, since production of this hormone is mediated by root N concentration which, in turn, is a function of N absorption from the soil and seasonal reallocation of tissue N. The form of applied N (*i.e.*, NO_3-N or NH_4-N) also seems to affect tillering. In this sense, it has been reported that spring wheat plants produced more tillers when grown in nutrient solutions containing N as an equal mixture of both forms than when grown with either form of N alone (Wang and Below 1995). This response has been attributed to the higher cytokinin/IAA ratio found in shoots of the former plants (Chen et al. 1998).

Phosphorus. A decrease in site filling as a consequence of phosphorus deficiency has been observed in tall fescue of temperate and Mediterranean origin (Martinefsky 2008). Similar reductions in tiller production have been observed in tall wheatgrass by Assuero and Ochner (not published) and in rice by Luquet *et al.* (2005). It is interesting to note that in early stages of phosphorus deficiency plants tend to accumulate sugars because of stunted shoot growth (Rodríguez *et al.* 1999), which seems rather in conflict with the carbon nutrition hypothesis on tillering.

Other mineral nutrients. Although N and P are the most important mineral nutrients in relation to tillering in grasses, potassium (K) usually promotes tiller production when N availability is adequate (Duble 2004). For instance, increased tiller number as a consequence of K fertilization has been reported in sorghum by Ogunlela and Yusuf (1988) and in rice by Bahmaniar and Ranjbar (2007). However, the response is generally moderate and, in same cases, no significant effects have been found (Silberbush and Lips 1991).

Ohki (1984) found that in wheat both manganese deficiency and toxicity reduced tiller number. Promotive effects of Mn on sugarcane tillering were reported by Jain *et al.* (2009). These authors also found a positive effect of calcium on tiller production. Among micronutrients, boron has sometimes been associated with increased tillering (Khan *et al.* 2006), but not always (Asad and Rafique 2000). Further research is needed to understand the mode of action of these nutrients.

Biotic factors

Plant rarely live as isolated individuals but rather establishing complex interactions with microorganisms. In fact, symbiosis is the typical state for large organisms (Stone *et al.* 2000; Schardl *et al.* 2004). For instance, densely colonized soil contains beneficial mycorrhizal fungi which associate with roots and provide plants with mineral nutrients in exchange for carbon. Also, bacteria in the rhizosphere can affect plant growth, nutrition, development and tolerance to stresses. Further, fungal endophytes systemically infect most of the plants of the major subfamily of temperate grasses, the Poöideae (Stone *et al.* 2000). Several of these plant–microbe interactions have been found to affect tiller development and longevity.

1. Mycorrhizae

Among many effects on plant growth, mainly through an improvement of plant P status, mycorrhizae have been found to alter biomass allocation (Newsham and Watkinson 1997). This includes promotion of tillering in *Agropyron* (Miller *et al.* 1987), *Lolium* (Hall *et al.* 1984) and *Holcus* (West 1996). The effect is not universal though, because in some cases no effects, or variable results depending on cultivars, have been reported (Jun and Allen 1991; West 1996).

In plants growing under stress conditions, tillering has been found to be favoured by mycorrhiza. For example, in the study of Ellis *et al.* (1985), water deficit reduced the number of tillers in non-mycorrhizal wheat plants but not in infected plants. It has also been observed that mycorrhizal plants of *Andropogon virginicus* L. showed stability in the number of tillers per plant when grown under a wide range of aluminium concentrations, showing 4.5-fold more tillers than nonmycorrhizal plants at the highest concentration studied (1000 mM Al) (Cumming and Ning 2003).

The promotive effect of mycorrhiza on tillering seems not to depend on the increased P status of the plants, since it has been shown to occur even in plants growing without P limitation (Brejda *et al.* 1993). It has been proposed, instead, that the effect on tillering may be mediated by altered host hormone balance (Miller *et al.* 1987; Koide 2000). The production of different plant growth–regulating substances by vesicular–arbuscular mycorrhizal fungi has been reported by Barea and Azcón Aguilar (1982).

2. Endophytic symbiotic fungi

Endophytic fungi are a group of fungi which live asymptomatically inside plant tissues. The most studied case is the mutualistic interaction between *Neotyphodium* spp. and temperate grasses such as perennial ryegrass (*Lolium perenne*) and tall fescue (*Festuca arundinacea*).

Environmental conditions in which plant grow can have important effects on the endophyte–grass interaction (Latch 1997). For example, under optimal plant growth conditions a higher tiller number has usually been found in endophyte–infected plants of *F. arundinacea* (Clay 1987; De Battista *et al.* 1990) and *L. perenne* (Latch *et al.* 1985; Clay 1987; Eerens *et al.* 1998; Cheplick 2008) than in uninfected ones, although this was not always the case (e.g., Maclean *et al.* 1993, working with *F. arundinacea*). However, when endophyte–infected plants were cultivated under restricted irradiance (Clay 1987) they produced fewer tillers than endophyte–free ones. Similarly, soil nutrient status seems to modify tall fescue growth responses to endophyte infection (Rahman and Saiga 2005). For instance, in low nutrient and water conditions endophyte infected plants of *F. pratensis* produced fewer tillers than uninfected ones (Ahlholm *et al.* 2002). Similarly, a lower tiller production in *F. arundinacea* endophyte–infected plants compared to uninfected plants was observed by Arachevaleta *et al.* (1989) when growing under low N availability. Nevertheless, Ravel *et al.* (1997) reported a greater number of tillers for infected than for uninfected plants of three *L. perenne* genotypes under N deficiency.

Evidently, the number of tillers is ultimately the result of tiller appearance and tiller survival, and both may be altered by endophytic fungi. It has been observed, for example, that endophyte infection seems to alleviate the negative effect of water deficit on tiller survival in *F. arundinacea*. This response could be related, at least in part, to a higher sugar content in tiller bases of endophyte–infected plants; these sugars might have come from carbohydrate remobilization from senescing organs (Assuero *et al.* 2006) (**Table 1**).

In another experiment, Assuero *et al.* (2000) reported that tiller number was reduced by endophyte infection in two *F. arundinacea* cultivars, one of temperate origin and another of Mediterranean origin, that had been artificially infected with two fungal endophyte strains (AgResearch isolate AR501 and the KY31 *N. coenophialum* strains). In this study, tillering of the Mediterranean cultivar was more negatively affected by endophyte infection than the temperate one and the AR501 *N. coenophialum* strain prompted a lesser depression of tiller number per plant than the KY31 strain. Differential responses on tiller production among tall fescue accessions have also been reported by Belesky *et al.* (1989). Hill *et al.* (1990) have suggested that these differential responses could be related to differences in the amount of IAA produced by the endophyte and/or plant genotype. Interestingly, De Battista *et al.* (1990) found that two strains of *N. coenophialum* produced IAA when grown in culture, one strain producing twice as much IAA as the other. Consequently, tillering will vary with particular plant genotype/endophyte strain combinations, depending on the precise details of the interaction between them (Latch 1997).

Because of the variability in the responses, Cheplick (2007) has suggested that endophyte–mediated effects on growth and allocation are clearly contingent on both environmental conditions and the genetic background of the specific host–endophyte associations used in field, greenhouse, or growth chamber investigations as the case may be.

Table 1 Effect of endophyte infection (E+: endophyte infected; E-: endophyte free) on reducing sugar concentration in sheaths and tiller number per pot for two water treatments (control and water deprivation for 20 days) in *Festuca arundinacea*. Values are averages of samplings performed at 7 and 20 days after water withholding imposition. For experimental details see Assuero *et al.* (2006).

Water treatment	**Tiller number per pot**		**Reducing sugars in sheaths (mg g^{-1} DW)**	
	E+	**E-**	**E+**	**E-**
Control	47.8	51.3	17.2	22.5
Water deprivation	38.5	28.2	42.3	24.9
S.E.M	5.3	3.7	6.7	1.0

3. Plant growth–promoting rhizobacteria (PGPR)

A promotive effect of the inoculation with the facultative endophytic N_2–fixing bacterium *Azospirillum lipoferum* on tiller number in rice was reported by several groups (Nayak *et al.* 1986; Bashan and Levanony 1990; Bashan and Holguin 1997; Kennedy *et al.* 2004; Kannaiyan and Kumar 2006). Also, another species of this genus, *Azospirillum brasilense*, has been found to enhance tillering in wheat by Creus (1997); this effect eventually resulted in an increased number of grains per unit area (Creus *et al.* 2004, 2009). Their results were later confirmed by Puente *et al.* (2008) who evaluated ten different *A. brasilense* strains from Argentina. In general, increased tiller number has been observed in parallel with a general enhancement of plant growth by inoculation with this bacterium.

Similar effects have been reported for inoculation with other PGPR in different experimental systems. For example, Niranjan *et al.* (2004) showed that when pearl millet seeds were bioprimed with *Pseudomonas fluorescens* plants exhibited enhancement of germination, seedling vigour, plant height, leaf area, tillering capacity, seed weight and yield.

In general, the production of hormones has been suggested to be one of the pathways by which PGPR stimulate plant growth. For instance, *Azospirillum* effects have been at least partly attributed to its ability to synthesize plant growth regulators such as auxins, gibberellins, cytokinins and ethylene (Tien *et al.* 1979; Strzelczyk *et al.* 1994; Thuler *et al.* 2003; Perrig *et al.* 2007). However the precise role of these hormones in tillering promotion is obscure, since not only hormones believed to be promotive (i.e., cytokinins) have been found to be produced by these bacteria, but also those that are believed to be inhibitory (i.e., auxins) have been reported. For instance, in Khalid *et al.* (2004) work with 30 different bacteria associated to wheat roots it was showed that different strains of PGPR produced *in vitro* variable amount of auxins (ranging from 1.1 to 12.1 mg L^{-1}) and that the addition of l–tryptophan to the culture media further stimulated auxin biosynthesis (ranging from 1.8 to 24.8 mg L^{-1}). In this study, IAA and indole acetamide (IAM) were identified as the major auxins in the culture filtrates of these rhizobacteria, and auxin production correlated well with growth promotion. Therefore the way by which PGPRs promote tillering deserves further study.

CONTROL OF TILLER DENSITY IN CANOPIES

Tillering cessation and tiller death

As canopy biomass increases over time, light interception increases and light intensity in the lower strata turns progressively lower. In parallel, the R: FR ratio decreases because of differential absorption of photons of these wavelengths by leaf pigments. So, it is the light environment that becomes the main environmental factor limiting plant growth. It is therefore not surprising that both light intensity and/or quality appear to play a decisive signalling role on the cessation of tillering, and eliciting tiller death, in dense canopies.

In general, tillering ceases earlier (in relation to stage of plant development) the higher the population density is. This may occur because at high plant densities both photosynthetically active radiation, or R: FR ratio, may fall below critical levels in the canopy. Discerning the relative importance of these two factors has been the subject of recent research. Working with spring wheat grown at different plant densities and contrasting light levels, Evers *et al.* (2006) found that at cessation of tillering both the fraction of light intercepted and the R: FR ratio at soil level were similar in all treatments. They proposed that cessation of tillering is induced when the fraction of PAR intercepted by the canopy exceeds a specific threshold (0.40–0.45) and the R: FR ratio drops below 0.35–0.40.

On the other hand, light quality has been found to be a more important factor than light intensity regarding tiller death. In their study with *Lolium perenne*, Ong and Marshall (1979) found that severe shading (i.e., 13 W/m^2) was required to trigger tiller death, while when plants were illuminated at only 70 W/m^2 none of the shaded tillers died, but rather they continued to produce new leaves and increase their dry weight albeit at a reduced rate. Lauer and Simmons (1989) studied tiller mortality in *Hordeum vulgare* in relation to shading and concluded that lack of light was not the factor that triggered tiller death, since initial signs of senescence in some tillers were noted early in the crop cycle, before appreciable shading of tillers occurred. They proposed that shading plays an auxiliary role in tiller senescence in barley, while early light quality changes would play a key role.

Further support of the involvement of light quality in tiller mortality was provided by the study of Sparkes *et al.* (2006). In their field experiments with wheat grown at contrasting plant populations and N availabilities, which created crops with widely varying tiller production and survival patterns, they investigated the 'triggering mechanism' responsible for the start of tiller death. They found no correlation between radiation available per shoot and the beginning of tiller death, while, on the other hand, the start of tiller death was closely related to the R: FR ratio measured at the base of the canopy. These authors proposed a critical R: FR ratio for the initiation of tiller death in winter wheat and also suggested that this critical R: FR ratio interacts with leaf N content – where leaf N content is higher, the critical R: FR ratio is lower, in other words, when more N is available, the canopy would achieve higher leaf area index before tiller death started and *vice versa*.

Size/density compensation

Most temperate pastures show some degree of adaptation to grazing management over a medium range of defoliation heights when they are subjected to it for a certain time. The relevant defoliation height range in which this adaptation can be observed, varies from species to species depending on natural tiller size and it does not take place under lax or severe defoliation. For example, perennial ryegrass is able to show high plasticity in terms of compensation between tiller population and tiller size under a wide range of grazing management conditions (Matthew *et al.* 2000).

In general, it has been assumed that defoliated pastures follow the self–thinning rule originally described by Yoda *et al.* (1963) which describes a density–depending upper limit to average shoot biomass per plant (Davies, 1988). According to this rule, a straight line of slope -3/2 is obtained when log of average shoot biomass per plant (i.e., log of tiller weight) is plotted against log of tiller population density (White and Harper 1970; Whittington 1984). This rule basically defines the shoot size and density combinations that render the maximum LAI that a particular species can maintain in a given environment (Matthew *et al.* 1995) (**Fig. 2**).

Another model for relationships between mass and density in resource-limited plants has been proposed by Enquist *et al.* (1998). It predicts that average plant size should scale as the -4/3 power of maximum population density, in agreement with some empirical evidence and comparable relationships in animals. However, the model assumes that rates of resource use in individual plants scale as approximately the 3/4 power of body mass, which has been seriously questioned by Kozłowski and Konarzewski (2004).

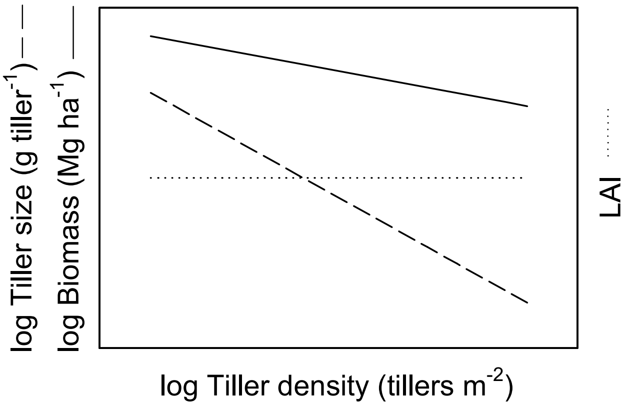

Fig. 2 Relationships between tiller size and tiller density according to the self–thinning rule. This rule assumes a maximum LAI sustainable by a particular species in a given environment and a slope of -3/2 for the log tiller size *vs* log tiller density relationship. Under this assumption, the slope for the log biomass per unit area *vs.* log tiller density relationship is -1/2.

The tiller size/density compensation (SDC) has been observed in many temperate and tropical forage grasses (Bircham and Hodgson 1983; Davies 1988; Matthew *et al.* 1995; Hernández Garay *et al.* 1999; Sbrissia *et al.* 2001; Hirata and Pakiding 2002; Sbrissia *et al.* 2003; Martínez Calsina *et al.* 2008). It occurs in response to changes in leaf area index (LAI) and in the state variables related with it (e.g., sward height, forage mass). Considering the sward structural characteristics that determine LAI, tiller density is the one that offers the plants the highest flexibility of adjustment to different grazing regimes. For example, in intensively grazed pastures, LAI is optimized through a high density of small tillers while in lenient grazed pastures through a low density of big tillers (Matthew *et al.* 2000). In grass swards SDC is one of the mechanisms that operates to buffer overall responses in terms of herbage production and utilization (Sbrissia *et al.* 2001). Consequently, the increase or decrease in tiller density would not be a precise indicator of pasture vigour itself and could, under certain circumstances, simply reflect the SDC in response to changes in defoliation intensity (Matthew *et al.* 1995).

Interestingly, experimental results in defoliated grass swards systematically indicate a steeper slope than -3/2 (Matthew *et al.* 1995; Sbrissia *et al.* 2001). This discrepancy has been attributed to changes in LAI due to growth and removal of leaf tissue and to the morphogenetic changes that tillers undergo when they adjust to different sward heights (Matthew *et al.* 1995). Consequently, Matthew *et al.* (1995) have proposed that defoliated swards maintained at different levels of herbage constant mass would show a SDC line with four phases. The first one corresponds to a low herbage mass in which tiller population density is too low to reach the SDC line; the second one corresponds to a variable leaf area self–thinning phase in which the slope is steeper than -3/2; the third one to the constant leaf area self–thinning at slope close to -3/2; and the last one to a constant herbage mass self–thinning with a slope of -1. The phase 3 of the curve would determine a ceiling to which the trajectories size/density would tend to move towards. The authors pointed out that the particular size/density coordinates at a given moment would be established by dynamic fluxes of herbage removal, leaf expansion and tiller appearance and death. It has been suggested that the point of transition between phases 2 and 3 would define the upper limit of plasticity of tiller size for a particular cultivar (Matthew *et al.* 2000).

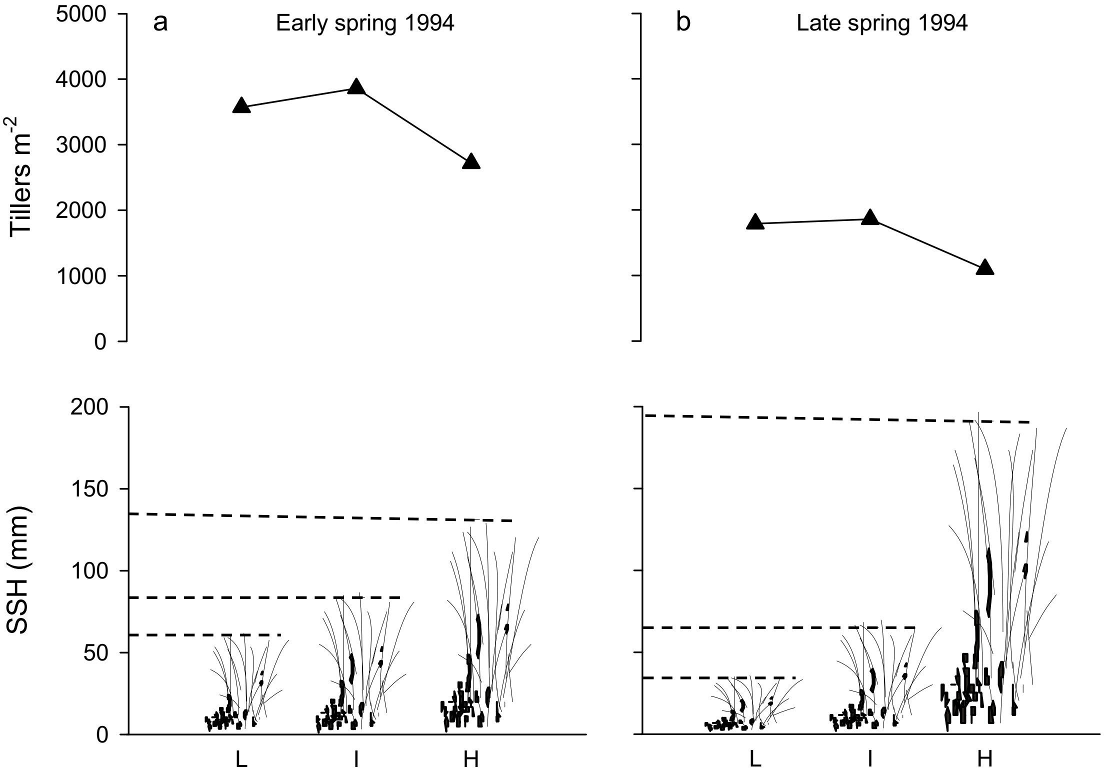

Fig. 3 Tiller density (tillers m^{-2}) in swards of tall fescue cv. 'Maris Kasba' continuously grazed at different sward surface heights (SSH; low = L, intermediate = I, and high = H) in (a) early and (b) late spring 1994. For methodological details see Agnusdei *et al.* (2007).

Temperate swards of the SE of Buenos Aires province, Argentina, consistently show lower tiller densities (lower than 4000 tillers m^{-2} in pure grass swards, Agnusdei *et al.* 2007) than those reported for perennial ryegrass swards in the UK (in the order of 10000-50000 tillers m^{-2} in pure grass swards, Tallowin *et al.* 1981) and even as compared with the values estimated for perennial ryegrass swards under New Zealand conditions (4000-11000 tillers m^{-2}, Xia *et al.* 1990). The difference could be partly explained by the larger tiller size of the most commonly–used species in Argentina, tall wheatgrass and tall fescue (Molina 1988; INDEC 1995) as compared with perennial ryegrass, since the principle of SDC determines large tillered species will have a lower tiller density. Furthermore, the lower availability of nutrients under the Argentinean conditions might also be involved in this response. For example, Laidlaw and Steen (1989) reported that perennial ryegrass tiller density increased in mixed swards with white clover in response to a higher N-fertilizer dose (9600 and 14150 tillers m^{-2} for N application rates of 60 and 360 kg N ha^{-1}, respectively).

Size density compensation was observed by Bertín *et al.* (1987) in tall wheatgrass swards subjected to continuous grazing, in which different herbage mass availabilities were maintained along time. For instance, in Autumn (end of March) tiller density was inversely related to herbage mass (1703 and 1035 tillers m^{-2} were recorded for herbage masses of 1500 and 3500 kg OM ha^{-1}, respectively). However, Agnusdei *et al.* (2007) did not find SDC in this species at low herbage masses; suggesting that the LAI was too low to reach the SDC line. A suppression of SDC has also been observed in strongly rhizomatous species of Chinese grasslands, perhaps because of assimilate sharing between connected tillers (Dr C. Matthew, personal communication). As suggested by Agnusdei *et al.* (2007), further research is needed to have a deeper understanding of tillering plasticity, especially under the limiting environmental conditions in which forage species are usually grown.

AGRONOMIC MANAGEMENT OF TILLERING

Tiller management in crops and swards

As stated above, in grain crops, species that develop tillers can respond plastically to the environment. Thus choosing a sowing density within the range in which plants may exert this compensatory ability leads to stable grain production provided the conditions are given for proper tiller survival, usually without causing significant unevenness in maturity in the crop (Hay and Kirby 1991). Besides, breeding of grain crops such as barley has given rise to new cultivars that have an increased ability to tiller and thus better adaptation to environmental stresses (Abeledo *et al.* 2004).

For swards, the theoretical approach of SDC seems to have practical implications (Matthew *et al.* 2000). In this sense it has been suggested that the perpendicular distance between the size/density coordinates and an arbitrarily located SDC line of slope -3/2 could be considered a productivity index when comparing similar pastures subjected to different defoliation treatments (Bahmani *et al.* 1997; Hernández Garay *et al.* 1999).

In **Fig. 3** the effect of sward defoliation height on continuously grazed tall fescue swards is shown. The treatment corresponding to the lowest sward defoliation height presented the highest tiller density. Although the physiological mechanism involved in this plastic response of grasses to frequent and severe defoliation (i.e., the reduction in size of individual tillers with a concomitant increase in tiller density) is not well understood, it has been suggested that the light quality variation, especially the R : FR ratio, is implicated (Lemaire and Chapman 1996).

Interestingly, and in contrast to what it takes place in successional vegetation associations that only move up the self–thinning line (i.e., population density decreases as individual size increases), tiller density in swards behaves reversible with respect to the size–density relationship, reflecting the dynamic nature of growth and senescence in grass swards, where there is a continual turnover of leaves and growth units (Lemaire and Chapman 1996). The practical consequence of compensatory changes between tiller size and tiller density in response to defoliation management is a relatively stable amount of total grass leaf production per unit area (Lemaire and Chapman 1996; Sbrissia *et al.* 2001). The degree to which such response could be extended to different forage grass species will depend on their ability to regulate size and density as well as on the stability of tissue turnover (Agnusdei *et al.* 2007). In this sense, it is important also to know the limit of this plastic response under severe defoliation regimes, since it has been demonstrated that a reduction in tiller density takes place under these circumstances (Bircham and Hodgson 1983; Robson *et al.* 1988; Hume 1991; Wan and Sosebee 2002). Consequently, long–term grazing experiments and detailed studies of tillering plasticity are needed to elucidate the effect of different grazing managements on the persistence and stability of herbage production with especial focus in grass species that are adapted to grow under the restrictive environments usually related to livestock production.

Modelling tiller dynamics

Models for tiller dynamics have been developed for practical purposes but also bearing in mind that they can provide insight into the factors that modulate tillering. Different approaches have been used for modelling tiller development and survival for both grain crops and swards.

Most dynamic models developed lately take advantage of the known relationships between environmental conditions, plant-plant interactions and agronomic practices that control bud outgrowth. For instance, in the 'Canopt' model, which simulates growth of either pure or binary mixture swards, tillering is constrained both by light transmission to ground level and by the availability of carbon and N by the plant, thus integrating the most important factors that control tiller outgrowth at the canopy level (Soussana and Oliveira Machado 2000). Further complexity is added when animal-plant interactions are included in these models (Gordon 2000).

In most of these models tillering is explained in a mechanistic manner, although some aspects may be treated in a stochastic way. For instance, in the 'Sistal' model of Lafarge and coworkers, in which the spatial distribution of tillers is simulated, tillering itself is mechanistic, and depends on the positions of the neighbouring tillers and environmental data, but tiller death is stochastic (Lafarge *et al.* 2005; Mazel *et al.* 2005).

More recently, models have been developed that also consider resource allocation as an important factor limiting tiller growth, such as "TILLERTREE" (Tomlinson *et al.* 2007). As these authors state, interactions between structural architecture and resource allocation affect the ability of plants to utilize environmental resources and thus can better explain tiller recruitment patterns and density-dependent mortality. In this model, allocation of resources is not calculated mechanistically, but rather by using a procedural algorithm based on object hierarchy and priority. In general, the models that integrate architecture and resource allocation as aspects of plant function are called 'Functional-structural models' (Sievänen *et al.* 2000; Tomlinson *et al.* 2007).

Luquet *et al.* (2006) described a functional–structural model called EcoMeristem, which was developed for cereals. EcoMeristem constructs the plant on the basis of an organogenetic body plan, which is driven by genetic behavioral norms of the state of meristems; these norms are in turn controlled by feedbacks of the plant resource status. In this model, plant resource status is expressed by a state variable called 'internal competition index' (Ic) which is calculated daily as the ratio of assimilate source (supply) over the sum of active sinks (demand). Interestingly, experimental test of this model has led to the conclusion that changes in Ic, which constitutes an internal signal analogous to sugar signalling, appeared to affect several physiological variables, including tiller initiation, thus adding support to the 'nutritional hypothesis' discussed above.

A further functional-structural model was developed by Evers and Vos (2007). Their 3D virtual model, called 'ADELwheat', studies the relationships between canopy architecture, light properties within the canopy, and tillering in spring-wheat plants. The model was calibrated for spring wheat, and validated for ground cover and leaf area index, using an independent dataset. Experimentally, they showed that new tillers ceased to appear when the fraction of light intercepted by the canopy exceeded 0.4, and that this threshold was independent of plant population density, shading, developmental stage of the plants and rank number of the tiller. Functional-structural modelling has also been applied to study ryegrass architecture (Verdenal *et al.* 2008). Potential applications of this type of modelling have been reviewed recently (Evers *et al.* 2010; Vos *et al.* 2010).

Nevertheless, entirely stochastic models have sometimes been attempted for simulating tillering. In the work by Mi *et al.* (2004), the generalization ability of 'neural networks' (NNs) in predicting rice tillering dynamics was tested. These authors found that NNs were able to extrapolate and predict the dynamics of tillering when the data were within the range of inputs of the training set. As these authors pointed out, NNs are not commonly used for modelling crop systems due not only to their highly empirical nature which makes them unable to extrapolate to untested datasets, but also because of the large amount of data needed to obtain robust parameter estimations. However, Mi *et al.* (2004) also remark that NNs, which have the advantage of their simple construction and parameter estimation procedures, may be an alternative to model tillering when systems are very complex, when there is a wide spatial and temporal variability and when responses are nonlinear.

CONCLUDING REMARKS

The present review has attempted to give an account of current day knowledge of the processes that control tiller outgrowth and the possibilities of its agricultural management. The wide array of environmental, endogenous and biotic effects that have been shown to affect tillering illustrates the physiological complexity of this process, which is undoubtedly affected by interactions between these factors and feedback loops as well. The tiller signalling process most likely involves cross-talks between different pathways, and should not be regarded as a linear cascade of events.

This, in turn, gives a hint of the difficulties arising when attempts are made to integrate such diversity of factors within a unifying theoretical basis that can account for all effects. Also, this complexity may indicate many shortcomings of the previously proposed hypotheses (i.e., the nutritional, hormonal and combined hypothesis) for the explanation of many observed effects, and why there are almost as many results in support as in conflict with them.

Nevertheless, continuous advance in the knowledge of these effects is enabling the elaboration of progressively more accurate models that provide a powerful tool for agronomic management of tiller dynamics, which in turn facilitate through their validation new insights on the control of tillering by the plant.

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