Growth and Development of Forage Plants

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Understanding the developmental morphology of forage plants is important for making good management decisions. Many such decisions involve timing the initiation or termination of a management practice at a particular stage of development in the life cycle of the plant. Physiological responses to defoliation and subsequent growth potential are affected by and strongly affect developmental morphology (Brueland et al., 2003; Parsons, 1988).

Leaf appearance rate during seedling development has been used to evaluate stand establishment and is strongly related to seedling root development (Moser, 2000). Leaf development on established tillers of perennial grasses can be used to time management practices such as defoliation, burning, fertilization, and growth regulator and pesticide application (Moore et al., 1991). Decisions regarding grazing and harvest management are often made on the basis of plant development (Brueland et al., 2003; Frank et al., 1993).

This chapter is concerned with the initiation, expansion, and maturation of leaves, stems, and roots and on the transition from vegetative to reproductive growth and production of reproductive tissues, all of which have profound effects on forage yield, quality, and stand longevity. Particular emphasis is given to the growth and development of leaves, which are the primary tissues for both photosynthesis and forage consumption.

Growth and Development of Plant Organs

The growth processes of each organ depend on cell division and elongation to provide the ultrastructure for plant tissue development and biomass accumulation. The elongated cells then differentiate to form specific organs and accommodate associated physiological functions. Interactions among leaf, tiller, and root meristems are coordinated to assure the orderly development of the plant.

Development of Leaf Structure

Production of leaf tissue requires the initiation, elongation, and maturation of new cells. Leaf development has been most extensively described for grasses because growth is mostly linear, resulting in large increases in leaf length accompanied by relatively small increases in width and thickness. In the grass leaf, cell division, elongation, and maturation zones occur sequentially along the base of the developing leaf. Subsequently, the youngest leaf tissues are located at the leaf base and the oldest at the leaf tip (Fig. 4.1).

At the very base of the leaf is the cell division zone, where modest elongation and repeated divisions of meristematic cells produce a region with average cell length of about 20 μm. Epidermal cell division is restricted to the basal 2 to 3 mm of the elongating leaf (Skinner and Nelson, 1995), whereas mesophyll cell division continues throughout the basal 10 to 15 mm of the leaf (MacAdam et al., 1989). Epidermal cells that have ceased dividing continue to elongate until they reach a mature cell length of 100 to 1000 μm depending on their position on the leaf and a host of environmental, management, and genetic factors (MacAdam et al., 1989; Erwin et al., 1994; Palmer and Davies, 1996; Schaufele and Schnyder, 2000). The length of the epidermal cell elongation zone is usually functionally related to leaf elongation rate.
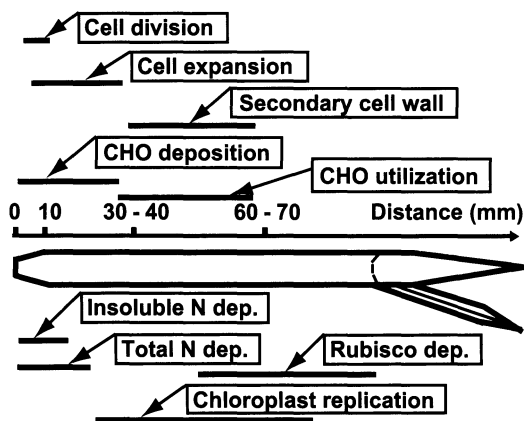
FIG. 4.1. Growth zones and zones of carbon and nitrogen deposition and utilization of elongating tall fescue leaf blades. (From Skinner and Nelson, 1995.)

Both cell division and elongation of grasses are affected by the environmental and management factors that alter leaf elongation. Thus, defoliation (Schaufele and Schynder, 2000), hypoxia (Smit et al., 1989), water deficits (Granier and Tardieu, 1999; Lecoeur et al., 1995), and nitrogen stress (MacAdam et al., 1989; Palmer et al., 1996) reduce cell division, cell elongation, or both. Nitrogen stress mainly reduces cell division. Water and other stresses have the greatest effect on cell division when leaves are small, whereas cell elongation can be affected by stress at any time during the leaf growth process.

Unlike grass leaves, which essentially grow in one direction, leaves of forbs, which include all legumes, have large increases in both length and width, which makes growth analysis more difficult. Also, cell division and elongation processes co-occur over a larger portion of the forb leaf and for a longer duration than in grass leaves.

Forb leaf growth can be considered a three-phase process (Granier and Tardieu, 1999). During the first phase, leaf area and cell number increase in tandem, similar to what occurs in the cell division zone of grasses. However, cell division in forbs, which occurs mainly along the leaf perimeter, can continue until the leaf is as much as 95% of its final size (Dale, 1988). The second phase of leaf expansion begins as the cell division zone advances outward, leaving the existing cells on the inward side to expand rapidly. In general, cell division ceases first at the leaf tip and continues longest at the leaf base. During the third phase, cell elongation rate declines and eventually ceases as all cells reach their final mature length.

The cell growth zone of grasses is generally located within a whorl of older leaf sheaths, which provides some protection against removal by grazing animals as well as buffering against adverse environmental conditions. In contrast, elongating forb leaves are more exposed to environmental stress (Radin, 1983). Thus, defoliation of forbs by grazers is more likely to remove all rapidly expanding leaf material, requiring regrowth to be initiated from new buds or small, undeveloped leaves. Grazing or mechanical harvest of grass leaves, however, tends to remove only mature leaf blades, leaving intact the fully developed and functional growth zones that can rapidly elongate the remaining leaf and reestablish photosynthetic area.

The biophysical processes associated with cell expansion have been summarized through a framework proposed by Lockhart (1965) that relates cell expansion to the driving force generated by water uptake and to the ability of cell walls to yield to that force. Water uptake is a function of cell membrane hydraulic conductivity, the osmotic pressure difference between a cell and its surrounding tissues, and cellular hydrostatic pressure (Cosgrove, 1986). Wall yielding, in turn, depends on the ability of the cell to generate sufficient turgor pressure to overcome the initial resistance to expansion (the yield threshold) and subsequent extensibility of cell wall components. Elongating cells have only a primary cell wall, so the yield threshold is low. Cells do not elongate after secondary cell wall material is deposited. While short-term cell elongation that increases plant size is controlled by cell wall yielding and water uptake, long-term growth in weight depends on carbon assimilation, nutrient absorption, and the synthesis of the structural cell wall components and other cellular constituents (Cosgrove, 1986).

Biomass Accumulation

The cell division and elongation zones are sites of high metabolic activity and dry matter accumulation (Fig. 4.2). The high biomass deposition in growth zones is mainly due to accumulation of water-soluble carbohydrates (Allard and Nelson, 1991) which can reach concentrations of 300 to 400 mg g^{-1} dry weight, or as much as five times the concentration of mature leaf tissue in field-grown plants (MacAdam and Nelson, 1987). Similarly, N content, which in the cell division zone can be very high, ranging from 30 to 75 mg g^{-1}, depending on N fertility regime (Gastal and Nelson, 1994), occurs mainly as proteins and nucleic acids. Given that N content by weight is nearly 16% for both compounds, proteins and nucleic acids can account for nearly half the dry matter in the cell division zone.

As with carbon and N accumulation, the growing region is also the strongest sink for the mineral nutrients K, Mg, Cl, Ca, and P (Meiri et al., 1992) and for water deposition (Schnyder and Nelson, 1987). The rapid influx of water associated with cell elongation means that fresh weight of the leaf elongation zone can be as much as 97%
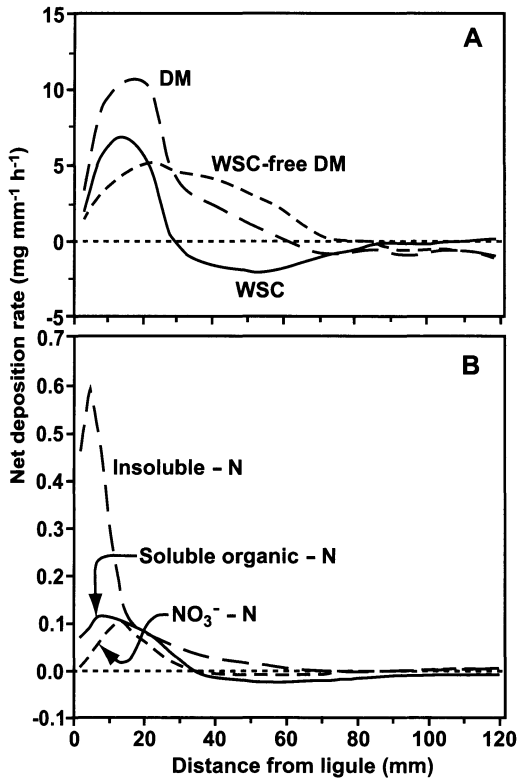
FIG. 4.2. Zones of net deposition and depletion for dry matter (DM), water-soluble carbohydrates (WSC), water-soluble carbohydrate-free dry matter (WSC-free DM), insoluble-N (polypeptides and nucleic acids), soluble organic-N (free amino acids, nucleic acids, and small peptides), and NO_3^--N in elongating tall fescue leaves. The sheath of the previous leaf would enclose the basal 100 mm. (Adapted from Allard and Nelson, 1991, and Gastal and Nelson, 1994.)

water (Meiri et al., 1992). The high water content, combined with the high percentage of nonstructural carbohydrate and N compounds and relatively low proportion of cell wall material, makes the grass growth zone extremely delicate and susceptible to damage if not protected by the enclosing sheaths of older leaves.

Nonstructural carbohydrate and N concentrations are much higher in the growth zone compared to mature tissues. As cells cease elongating and enter the cell maturation zone, the nonstructural carbohydrates can be recycled to provide energy and carbon skeletons for secondary cell wall formation (Allard and Nelson, 1991), whereas recycled-N can be used for synthesis of photosynthetic

proteins (Gastal and Nelson, 1994). Even though the rate of dry matter accumulation is greatly reduced compared to elongating cells, non-elongating cells continue to differentiate and accumulate additional biomass, mostly as secondary cell wall material and in sclerenchyma tissue.

As cells mature and their photosynthetic apparatus develops, they undergo a transition from a carbon sink to a carbon source for the rest of the leaf. Similarly, as leaf development continues, the leaf as a whole ceases to be a sink and becomes a source for younger leaves. This change, which marks a fundamental transition in leaf physiology, tends to occur in forb leaves when they reach about 30% to 60% of their final length and is concurrent with the maturation of minor veins in the leaf (Turgeon, 1989). This transition is marked by the cessation of carbohydrate import from mature leaves and is usually, but not necessarily, associated with the achievement of positive carbon balance in the leaf, i.e., when photosynthesis first exceeds the growth and respiratory needs of the leaf (Turgeon, 1984). This can occur simultaneously for several leaves (Gagnon and Beebe, 1996) or for only one leaf at a time (Turgeon and Webb, 1973).

The sink-to-source transition occurs later in the development of grass leaves than it does for forbs. Thus, tall fescue leaves remain a sink until they have reached about 80% of their final length (Bregard and Allard, 1999). The delayed transition in grasses occurs because early development of the blade occurs in relative darkness within the whorl of mature sheaths, whereas all stages of forb leaf development occur under full exposure to light.

Following defoliation, leaf elongation of grasses often continues at rates equal to or greater than elongation rates prior to defoliation (Morvan-Bertrand et al., 2001). This increased elongation occurs at the same time that dry matter and carbohydrate concentrations in the growth zone decrease (De Visser at al., 1997). Increased elongation is driven by continued high rates of water deposition in the growth zone accompanied by the hydrolysis of fructan, a polymer of fructose that serves as a storage carbohydrate, to support construction of structural materials (Volenec, 1986).

The increase in leaf length is accompanied by reduced growth in leaf width and thickness. This shift in growth to produce thinner leaves allows for more rapid establishment of functional leaf area per unit of substrate to quickly capture sunlight and reestablish a positive carbon balance for the plant. Similarly, narrow and thin leaves occur at low irradiance, allowing increased leaf elongation to occur despite reduced dry matter import into the elongation zone (Schnyder and Nelson, 1989; Sanderson and Nelson, 1995). Leaves of forbs also show an increase in specific leaf area (area wt^{-1}) under shade, resulting in larger but thinner leaves (Dale, 1988). Frequent cutting increased white clover leaf elongation rates (Li, 2000), although the effect on leaf thickness was not reported.

Table 4.1. Synchronization of major developmental transitions involving epidermal cell division and elongation during initiation and appearance of tall fescue leaves and tillers. The cotyledon is located at node 1 and the coleoptile at node 2. Thus, leaf 2 develops from node 4, leaf 3 from node 5, and so on.

Haun Index	Node	Event	Haun Index	Node	Event
1.9	4	Division in sheath of leaf 2 ends	2.8	5	Division in sheath of leaf 3 ends
2.0	4	Elongation of tiller 1 begins	2.7	5	Elongation of tiller 2 begins
1.9–2.1	5	Ligule is initiated on leaf 3	2.8–3.0	6	Ligule is initiated on leaf 4
2.0	6	Elongation begins for blade 4	2.8	7	Elongation begins for blade 5

Source: From Skinner and Nelson, 1994b.

Location, Activity, and Synchronization of Meristems

In addition to growth of individual leaves, forage production and stand longevity rely on initiation of new leaves and stems (tillers). The basic unit of grass development is the *phytomer*, which consists of a leaf, internode, axillary bud, and one or more root primordia. Within each phytomer, the leaf primordium produces both a blade and sheath, separated by a membranous layer of cells called the ligule, while a branch or tiller arises from the axillary bud (Skinner and Nelson, 1994b). The internode remains relatively short during vegetative growth but elongates to elevate the inflorescence during reproductive development. Elongation of the internode tends to inhibit axillary bud elongation as evidenced by a strong negative correlation between axillary bud and internode length (Williams and Langer, 1975). Root elongation follows tiller initiation within a given phytomer, generally about three phyllochrons after initiation of the leaf blade (Carman and Briske, 1982; Klepper et al., 1984).

As with leaf growth, developmental relationships among leaves and tillers have been more extensively studied in grasses than in forbs. Generally, grass tillers begin to elongate after the leaf that originates from the same node as the tiller has reached full size, giving rate of leaf appearance ultimate control over the rate of tiller appearance (Davies and Thomas, 1983; Skinner and Nelson, 1994a).

Major transitions in leaf and tiller development in tall fescue appear to be synchronized among at least three adjacent nodes (Table 4.1). Cessation of cell division in the leaf sheath at a given node, e.g., node 4, is accompanied by the initiation of cell division and elongation of the tiller bud at the same node. Simultaneously, the transition between blade and sheath formation begins at the next youngest node (node 5), while elongation of the new blade begins at node 6 (Table 4.1).

The transition between blade and sheath elongation for a given leaf occurs gradually as the ligule, which is visible early in development and marks the boundary between blade and sheath tissue, moves through the leaf elongation zone (Schnyder et al., 1990). The sheath first forms near the base of the cell division zone when the blade of the same leaf is 20% or less of its final length (Skinner and Nelson, 1994b). Elongation of the sheath is initially slow compared to the blade, but as sheath elongation rate increases the ligule above it is displaced through the elongation zone, causing blade elongation to decrease as cell supply is depleted.

The close relationship between leaf and tiller initiation makes it possible to mathematically describe tiller production as a function of leaf appearance rate and of site filling, which provides a measure of the ability of axillary buds to develop into new tillers (Davies, 1974). Assuming that buds are produced in each leaf axil and that each bud has the potential to develop into a new tiller, i.e., fill the site, Davies (1974) determined that tiller number can potentially increase by a factor of 1.618 during each leaf appearance interval on the main stem. However, Neuteboom and Lantinga (1989) pointed out that tiller buds can also develop in the axil of the prophyll, which is a small scaly leaf at the base of each tiller.

When prophyll tillers are taken into account, tiller number has the potential to increase by a factor of 2.0 for each leaf appearance interval. In other words, the number of tillers per plant can double with the appearance of each new leaf on the main stem. This potential tiller appearance rate assumes that the new tiller appears in the axil of the second-youngest fully emerged leaf on the parent tiller. An analogous concept to site filling called nodal probability, with values ranging from 0 to 1, has been developed to describe the probability of a tiller developing at any individual site (Matthew et al., 1998).

During periods of rapid tiller development, tillers appear in highly synchronized cohorts with the potential size of each cohort doubling with each successive leaf appearance interval (Fig. 4.3). Tiller buds that lose synchronization with the remainder of the cohort become progressively less likely to appear (Skinner and Nelson, 1992). Growth of tiller buds appears to be constrained by surrounding tissues such that tillers that emerge must escape from the cavities in which they develop before be-
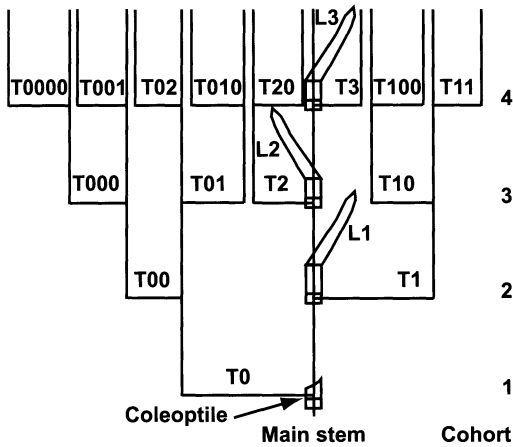
FIG. 4.3. Appearances of tiller cohorts are synchronized with leaf appearance on the main stem (MS). Tillers (T) are named for the leaf axil in which they appear; T0 appears in the axil of the coleoptile and tillers; T×0 appears in the prophyll axil of each tiller. Tillers within a cohort that emerge do so at nearly the same time, usually within 0.6 to 1.0 phyllochron after appearance of the main-stem leaf that is two phytomers younger than the tiller, i.e., T1 appears after appearance of L3. (Adapted from Skinner and Nelson, 1992.)

coming trapped by the maturation and hardening of surrounding tissues (Williams and Langer, 1975). This suggests that a window of opportunity exists for each tiller to emerge and that delayed development results in a missed opportunity for rapid growth and eventual emergence.

Adventitious root development is also closely tied to leaf and tiller development since these roots originate from nodes associated with leaves and developing tillers. Adventitious roots usually begin to appear when the main stem or individual tiller has about three developed leaves, and then appear sequentially at each successive node about three plastocrons after the leaf at that node first appears (Carman and Briske, 1982; Rickman et al., 1985). Appearance of roots on a tiller is generally an indication that the tiller has become independent of the main stem and is a necessary step for long-term survival of the tiller. Severe defoliation during initial tiller development may decrease tiller root establishment, causing newly initiated tillers to die (Carman and Briske, 1982).

As with grasses, growth and development of legumes and forbs also occur through the sequential production of phytomers consisting of a leaf, internode, axillary bud, and one or more root primordia (Gautier et al., 2001). As with grasses, the leaf from a given phytomer for alfalfa expands to nearly full size before the associated internode begins rapid extension (Brown and Tanner, 1983). In crown-forming species such as alfalfa, axillary bud development from the cotyledonary node and other basal nodes on developed stems results in the formation of a well-defined crown containing multiple stems (Barnes and Sheaffer, 1995). Regrowth following defoliation can occur from basal axillary buds located on the crown or from upper axillary buds along the stem. In contrast, clonal species such as white clover have two distinctive morphological stages. First, a seminal taproot develops after establishment and is followed by stolon growth to form a dispersed clonal stage 1 to 2 yr later (Brock et al., 2000). Death of the taproot and primary stolon initiates the fragmentation of the initial plant into a number of independent clones that are rooted at nodes of the surviving stolons. These clonal plants can have a lateral spread of 1 m or more (Brock et al., 2000; Gustine and Sanderson, 2001).

Describing and Quantifying Morphological Development

Several systems have been developed to describe developmental stages of forage species and have been used as aids to help schedule management practices.

Developmental Stages

The life cycles of forage plants are characterized by distinct changes in plant morphology. The ontogeny of most forage plants involves seedling, vegetative, and reproductive stages of development. These occur in a predictable manner and are useful for describing the maturity of individual plants as well as populations or stands.

The *vegetative stage* encompasses the period during which major activity is in leaf growth and development, which can be characterized by the successive appearance of leaves. In grasses, stem internodes are laid down and differentiated during this period but do not elongate. In many forbs, including most forage legumes, stem growth occurs throughout the vegetative stage. However, in others, such as chicory or plantain, internodes remain short and a leafy rosette is formed.

The interval of time between appearances of successive leaves is called the *phyllochron* and is sometimes used as an index for describing vegetative growth (Wilhelm and McMaster, 1995). During the time a tiller or stem remains vegetative, the apical meristem is indeterminate and, theoretically, can produce an infinite number of new nodes and leaves. In grasses, stem elongation, a process commonly referred to as *jointing*, is considered a transition state between vegetative and reproductive development (Waller et al., 1985). Elongation of stem internodes is accompanied by differentiation of the shoot apex meristem into the inflorescence.

Table 4.2. Morphological descriptors for growth stages of forage grasses and legumes

Terminology	Definition
Grasses	
First growth	
Vegetative	Leaves only; stems not elongated
Stem elongation	Stems elongated
Boot	Inflorescence enclosed in flag leaf sheath and not showing
Heading	Inflorescence emerging or emerged from flag leaf sheath, but not shedding pollen
Anthesis	Flowering stage; anthers shedding pollen
Milk stage	Seed immature, endosperm milk
Dough stage	Well-developed seed; endosperm doughy
Ripe seed	Seed ripe; leaves green to yellow brown
Postripe seed	Seed postripe; some dead leaves; some heads shattered
Stem-cured	Leaves cured on stem; seed mostly cast
Regrowth	
Vegetative	Leaves only; stems not elongated
Jointing	Green leaves and elongated stems
Late growth	Leaves and stems weathered
Legumes	
Spring and summer growth	
Vegetative (or prebud)	No buds visible
Bud	Buds visible, but no flowers
First flower	First flowers appear on plants
Bloom (flower)	Plants flowering
Pod (or green seed)	Green seedpods developing
Ripe seed	Mostly mature brown seedpods with lower leaves dead and some leaf loss
Fall recovery growth	Vegetative or with floral development

Source: From Metcalfe and Nelson, 1985.

The reproductive stage begins with the initiation of inflorescence development and continues through seed ripening and shatter. Seed ripening is sometimes considered a distinct developmental period, in which case the reproductive period terminates with fertilization (Moore and Moser, 1995).

Metcalfe and Nelson (1985) described several growth stages that are commonly used to indicate the maturity of grass and legume forages (Table 4.2). These useful descriptors are easily understood and applied, but they do not provide a way to quantify maturity, which is essential for mathematical modeling of developmental morphology and describing maturity of populations of forages.

Quantifying Developmental Morphology

A number of methods have been developed to describe and quantify morphological development of forage species. These systems share some common characteristics, including a defined series of morphological descriptors that have an associated numerical index. The numerical index can be used to develop mathematical relationships between forage maturity and variables such as forage quality and yield (Kalu and Fick, 1981; Hendrickson et al., 1997). Conversely, maturity indices can be used as dependent variables to predict forage maturity based on chronology or accumulated heat units (Mitchell et al., 1997; Sanderson and Moore, 1999). These phenological relationships are useful for timing management practices that depend on maturity.

Attempts to develop a universal system for describing and quantifying morphological development of forage crops have not been successful (Sanderson et al., 1997). A committee appointed by the Crop Science Society of America to identify and recommend a growth-staging system that was generally applicable to crops and weeds was unsuccessful in identifying any that could be used with acceptable precision (Frank et al., 1997). Instead, the committee recommended a number of growth-staging systems specific to individual crops, including forages (Table 4.3).

Alfalfa

The recommended system for staging alfalfa was originally developed by Kalu and Fick (1981) and was later

Table 4.3. Staging systems recommended for use with forage crops

Forage Crop	Reference
Alfalfa	Kalu and Fick, 1981; Fick and Mueller, 1989
Cool-season grasses	Haun, 1973; Moore et al., 1991
Red clover	Ohlsson and Wedin, 1989
Stoloniferous grasses	West, 1990
Warm-season grasses	Moore et al., 1991; Sanderson, 1992

Source: Adapted from Frank et al., 1997.

modified by Fick and Mueller (1989). It recognizes 10 stages of development that occur within four growth phases (Table 4.4). Vegetative stages consist of leaf and stem development and are defined in terms of stem length. Stages during flower-bud development are defined by the appearance and number of flower buds on the stems. Flowering stages correspond to the number of open flowers present on a stem. Seed production stages are defined by the number and color of seedpods. Many of these morphological descriptors are specific to alfalfa but can be modified for other species. However, they are generally not directly applicable to most other legumes.

Red Clover

The staging system developed by Ohlsson and Wedin (1989) for red clover is an adaptation of the alfalfa system (Table 4.4) with descriptors for vegetative and flower-bud development stages being nearly identical for the two systems. The main differences are in the flowering and seed production stages, reflecting differences in inflorescence morphology between the species.

Ohlsson and Wedin (1989) also evaluated another system for red clover that includes 18 stages and has the advantage of having more logical morphological descriptors. It performed well. The 10-stage systems for both alfalfa and red clover include length descriptors that are not strictly morphological (Fick and Mueller, 1989). Stem length varies among cultivars of both species, so

Table 4.4. Developmental stages, numerical indices, and morphological descriptors for alfalfa and red clover

Index	Stage	Alfalfa Descriptors[a]	Red Clover Descriptors[b]
Vegetative phase			
0	Early vegetative	Stem length ≤15 cm, no buds, flowers, or seedpods	Stem length ≤15 cm, no buds, flowers, or seedpods
1	Mid-vegetative	Stem length 16–30 cm, no buds, flowers, or seedpods	Stem length >15 to <30 cm, no buds, flowers, or seedpods
2	Late vegetative	Stem length ≥31 cm, no buds, flowers, or seedpods	Stem length ≥31 cm, no buds, flowers, or seedpods
Flower bud development			
3	Early bud	1–2 nodes with buds, no flowers or seedpods	1–2 nodes with buds, no flowers or seedpods
4	Late bud	≥3 nodes with buds, no flowers or seedpods	≥3 nodes with buds, no flowers or seedpods
Flowering phase			
5	Early flower	1 node with 1 open flower, no seedpods	Open flower (standard open) on main stem, no seed in flower head
6	Late flower	≥2 nodes with open flowers, no seedpods	Open flowers (standard open) on main and axillary stems, no seed in flower heads
Seed production			
7	Early seedpod	1-3 nodes with green seedpods	Seeds developing in the flower of the main stem
8	Late seedpod	≥4 nodes with green seedpods	Seeds developing in the flowers of the main and axillary stems
9	Ripe seedpod	Nodes with mostly brown mature seedpods	Sepals of flowers brown

[a]From Fick and Mueller, 1989.
[b]From Ohlsson and Wedin, 1989.

vegetative stages of development may be inconsistent with regard to the number of nodes and length of internodes of the plant. Thus, Ohlsson and Wedin (1989) recommended using the 18-stage system for research studies on red clover, especially those focused on early stages of development.

Cool-season Grasses

The Haun system was developed to quantify wheat development (Haun, 1973) but has been successfully used to quantify development of cool-season perennial grasses (Frank et al., 1993). Numerical indices correspond to the number of developed leaves on the primary tiller; that is, tillers with one, two, and three fully expanded leaves are assigned index values of 1, 2, and 3, respectively. Partially expanded leaves are assigned a fractional value relative to the most recent fully expanded leaf. For example, a tiller with three fully expanded leaves and a developing fourth leaf that is one-half the length of the third would be assigned an index of 3.5. The Haun system applies only to

leaf development up through stem elongation stages and, therefore, its use is limited primarily to vegetative growth. It has been used successfully to predict grazing readiness of native and introduced pastures (Frank et al., 1993).

Moore et al. (1991) developed a system for quantifying the developmental morphology of grasses for use in forage and range management studies. Their system, called the Nebraska system, is based on the ontogeny of individual tillers, which is divided into four primary growth stages: (1) vegetative, (2) elongation, (3) reproductive, and (4) seed ripening (Table 4.5). Within each primary stage, substages are defined that correspond to specific morphological events. Thus, each growth stage consists of a primary and secondary stage and has a numerical index associated with it that can be used for quantitative purposes. The vegetative and elongation substages are open ended, with the number of substages being equivalent to the number of morphological events (N) that occur for that species or environment. The reproductive and seed-ripening primary stages each have six secondary or sub-

Table 4.5. Growth stages of perennial grasses, their numerical indices, and descriptions

Stage	Numerical Index	Description
Vegetative Stage — Leaf Development		
VE or V0	1.0	Emergence of first leaf
V1	$(1/N^a) + 0.9$	First leaf collared
V2	$(2/N) + 0.9$	Second leaf collared
Vn	$(n/N) + 0.9$	Nth leaf collared
Elongation Stage — Stem Elongation		
E0	2.0	Onset of stem elongation
E1	$(1/N) + 1.9$	First node palpable / visible
E2	$(2/N) + 1.9$	Second node palpable / visible
En	$(n/N) + 1.9$	Nth node palpable / visible
Reproductive Stage — Floral Development		
R0	3.0	Boot stage
R1	3.1	Inflorescence emergence / 1st spikelet visible
R2	3.3	Spikelets fully emerged / peduncle not emerged
R3	3.5	Inflorescence and peduncle fully elongated
R4	3.7	Anther emergence / anthesis
R5	3.9	Post-anthesis / fertilization
Seed Development and Ripening Stage		
S0	4.0	Caryopsis visible
S1	4.1	Milk
S2	4.3	Soft dough
S3	4.5	Hard dough
S4	4.7	Endosperm hard / physiological maturity
S5	4.9	Endosperm dry / seed ripe

Source: From Moore et al., 1991.

[a] Where n equals the event number (number of leaves or nodes) and N equals the number of events within the primary stage (total number of leaves or nodes developed). General formula is $P + (n/N) - 0.1$, where P equals primary stage number (1 or 2 for vegetative and elongation, respectively) and n equals the event number. When $N > 9$, the formula $P + 0.9(n/N)$ should be used.

stages, numbered 0 through 5, which pertain to particular events in the ontogeny of the primary shoot or tiller. The substages for these primary stages describe specific events that occur similarly in most grasses.

In addition to the numerical index, the Nebraska system associates a mnemonic code with each growth stage. The codes can be easily memorized and are useful for applying the system in the field. Each code consists of two characters: a capital letter denoting the primary growth stage, followed by a number denoting the substage within that primary stage. Growth stages as denoted by the mnemonic codes are consistent across species.

Warm-season Grasses

The Nebraska system (Moore et al., 1991) described above was developed for both warm- and cool-season grasses and works well for both (Mitchell et al., 1998). Another system recommended for warm-season grasses is the TAES system, which was developed specifically to describe and quantify development of determinate and indeterminate flowering warm-season bunchgrasses (Sanderson, 1992). It uses a numerical index similar to the Haun (1973) scale during vegetative development.

The numerical index of the TAES system is discontinuous between the vegetative and stem elongation stages, and between the elongation and reproductive stages of development. These discontinuities result from inclusion of enough indices within a major growth stage to allow for variation in development that occurs among species and growth environments. The Nebraska system avoids this problem by linearizing indices within the vegetative and elongation growth stages according to the number of morphological events that occur within them (Moore et al., 1991).

Discontinuous scales can result in significant numerical shifts in transitions between stages, resulting in nonlinear responses (Sanderson et al., 1997). Another problem occurs when demographic statistics are calculated for a population of tillers that include discontinuous growth stages. Under these circumstances it is possible to calculate a mean index associated with a morphological descriptor that does not occur for the species. For example, the mean stage might indicate a stem with seven nodes for a species that elevates only four (Moore and Moser, 1995).

Discontinuous scales can be useful, but caution should be exercised when interpolating across discontinuous growth stages. Indeed, the TAES system may be more useful than the Nebraska system for detailed studies on vegetative development because it uses a greater number of indices to describe growth during this period.

Stoloniferous Grasses

Grasses that produce predominantly horizontal stems cannot be described well using systems recommended for staging upright grasses. West (1990) developed a system for staging the development of bermudagrass that is applicable to other stoloniferous grasses. The primary difference from other systems is that vegetative stages are defined in terms of development of nodal zones rather than leaves. Descriptors for other stages of development are analogous to other grass staging systems, although the coding of the numerical index to descriptors varies among systems.

Demography

Numerical indices are useful for describing the demography of forage populations (Mitchell et al., 1998). This is important because often there is significant variation in morphology among plants comprising a population of a given species. Many important forage species are cross-pollinated and are propagated as synthetic cultivars that represent an assemblage of related genotypes (Chap. 28). Hence, there is more variation in developmental morphology within a population of perennial forages than would be observed with most annual grain crops (Moore and Moser, 1995).

Most staging systems applied to perennial forage crops are not applied at the whole plant or population level. Rather, they are applied to modular subunits, which are usually tillers in grasses and stems in legumes. This approach arises from the difficulty in distinguishing among plants in dense swards and the fact that in many species significant variation in maturity exists among subunits arising from a single plant. Thus, a forage plant can be considered a metapopulation of tillers to which demographic principles can be applied (Harper, 1980; White, 1979).

A notable exception to the above approach would be in studies of seedling development where the whole plant is the subject of interest. For example, Moser et al. (1993) developed a system for describing the development of grass seedlings that includes morphological descriptors for the whole plant, including roots.

The developmental morphology of a population of established forage plants can be characterized using numerical indices and descriptive statistics. A random sample of plants (or tillers) is selected and the growth stage of each individual in the sample is determined. The mean developmental stage can be calculated using the following equation:

$$MSC = \sum_{i=1} \frac{S_i \times N_i}{C}$$

Where MSC = mean stage count, S_i = growth stage index, N_i = number of plants in stage S_i, and C = total number of plants in the sample population (Moore et al., 1991). A weighted mean stage, referred to as mean stage weight

(MSW), can be calculated using this formula by replacing N with the dry weight of the plants in each stage and C with the total dry weight of the sample (Kalu and Fick, 1981). The MSW gives more influence to later growth stages since plants accumulate more dry weight as they mature. Therefore, MSW accounts for the contribution of each growth stage to the total biomass of the population. In some studies, MSW has been shown to be more useful than MSC for quantifying the relationship between maturity and forage quality (Ohlsson and Wedin, 1989).

The standard deviation of the MSC (S_{MSC}) is useful for interpreting the variability in maturity existing within a population of one or many forage species (Moore et al., 1991). Higher values of S_{MSC} indicate greater variation in maturity within the population. Small values of S_{MSC} indicate that most plants in the population are of similar maturity and have a value near the MSC. The S_{MSC} can be calculated from the formula

$$S_{MSC} = \sqrt{\sum_{i=1} \frac{(S_i - MSC)^2 \times N_i}{C}}$$

using parameters from the equation for MSC. Calculating a similar statistic for MSW is not as easy because it is the product of two variables (stage and weight), which are not independent (Moore et al., 1991).

The MSC and S_{MSC} were used to describe maturity of tiller populations of intermediate wheatgrass and big bluestem in mid-June near Mead, NE, and staged using the Nebraska system (Table 4.5). The four vegetative stages, V1, V2, V3, and V4, for big bluestem coded numerically as 1.15, 1.40, 1.65, and 1.9 (Fig. 4.4). The MSC was 1.51, indicating the average tiller in this population had between two and three fully collared leaves. Intermediate wheatgrass, a cool-season grass, had a higher MSC, indicating it was more mature on the sampling date. The higher S_{MSC} indicated it also had a wider range of stages present than did big bluestem, a warm-season grass.

Systems for staging developmental morphology can be used to quantify and describe the seasonal demography of forage populations. A demographic analysis of a population of intermediate wheatgrass tillers (Fig. 4.5) shows the change in number of tillers in each primary growth stage with respect to time. At the first four sampling dates, all tillers were vegetative. In a period of 1 wk, however, over half the tillers began to elongate and in another 3 to 4 wk some tillers were advancing into reproductive stages. Coincident with the onset of elongation was an increase in tiller mortality that resulted in nearly a 40% decrease in tiller density by day 149.

Interestingly, only a relatively small proportion of tillers actually advanced through the reproductive to seed
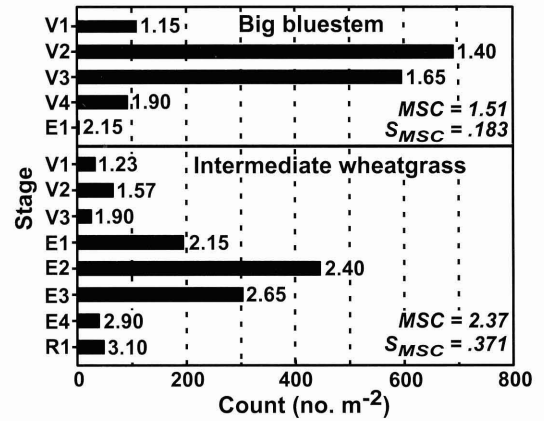

FIG. 4.4. Frequency distribution of tiller growth stages for big bluestem and intermediate wheatgrass populations sampled in mid-June near Mead, NE. (From Moore and Moser, 1995.)
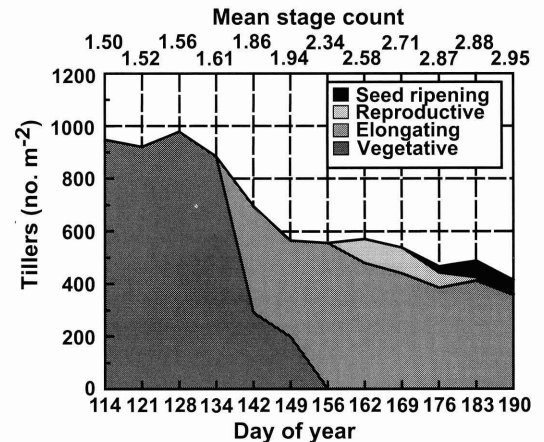

FIG. 4.5. Developmental morphology and demography of an intermediate wheatgrass tiller population during the 1991 growing season near Mead, NE. (From Moore and Moser, 1995.)

ripening stages (Fig. 4.5). This population would have been described as fully headed based on visual observation during the reproductive and seed ripening phases when, in reality, fewer than 20% of the culms produced inflorescences. It is evident from this example that MSC should not be interpreted as the actual growth stage of the population but rather as the mean representing all the growth stages present in a population.

Predicting Developmental Morphology

Continuous numerical indices can be used to develop mathematical relationships between developmental stages and temporal and climatic variables. These relationships can be descriptive or predictive in nature, depending on the intended use of the resulting equations. In many cases, staging systems are used to accurately describe the development of forages within the context of a specified period of time with no intention of making predictions about the development of the forage at another time (Brueland et al., 2003; Sanderson, 1992). The goal is simply to provide a clear account of the maturity of the forage in relation to other factors of interest.

Another, potentially more powerful use of numeric indices is the development of phenological models for predicting forage development. Such models relate developmental morphology to climatic variables, such as photoperiod and accumulated heat units. Development of robust phenological models would enable forage producers to predict the occurrence of important morphological events using climate data. This is significant because many important management decisions are based on maturity of the forage. Unfortunately, few such models have been developed and validated for general use.

Empirical models for predicting morphological development of switchgrass and big bluestem have been developed and validated for use in the central US (Mitchell et al., 1997; Sanderson and Moore, 1999). Equations were developed for predicting MSC using the Nebraska system as a function of day of year and growing degree days. Under Nebraska conditions, switchgrass development was best predicted (r^2 = 0.96) using a linear equation based on day of the year. This relationship indicates that photoperiod is the main determinant of switchgrass morphological development (Mitchell and Moser, 2000). In contrast, big bluestem development was more accurately predicted (r^2 = 0.83) using a nonlinear equation based on growing degree days, suggesting that its development is less determinate than that of switchgrass.

Prediction equations were developed in Nebraska based on data collected over two growing seasons for 'Trailblazer' switchgrass and 'Pawnee' big bluestem (Mitchell et al., 1997). The equations were subsequently validated over two additional growing seasons in Nebraska and Kansas (Fig. 4.6). The switchgrass equation was further evaluated for use with 'Cave-in-Rock' and 'Kanlow' switchgrass in Iowa, and Cave-in-Rock and 'Alamo' switchgrass in Texas (Sanderson and Moore, 1999). The Nebraska equation performed well for predicting development of the two cultivars in Iowa but did not do as well in Texas due to large differences in daylength and climate. These studies suggest that there is good potential for developing reliable and robust equations for predicting grass development on a regional basis.
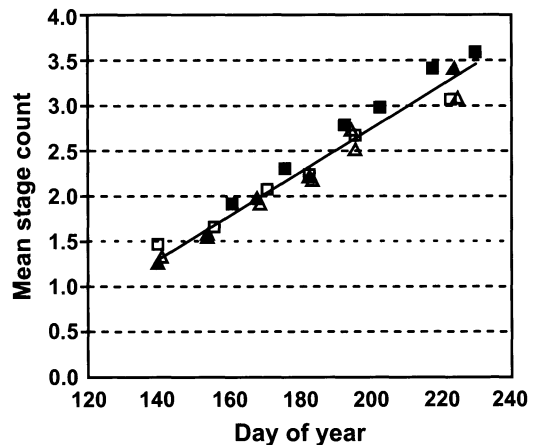

FIG. 4.6. Actual and predicted mean stage count of 'Trailblazer' switchgrass grown in Kansas (■) and Nebraska (△) during 1992 *(open symbols)* and 1993 *(closed symbols)*. Predicted MSC = 0.024(Day) − 2.063. (Adapted from Mitchell et al., 1997.)

Developing similar equations for important forage species within different regions could be of great benefit to producers.

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