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Growth and Development, from: *Forages: The Science of Grassland Agriculture, Volume II*

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CHAPTER

7

Growth and Development

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Introduction

The growth and development of forage plants is an amazing process. In some annual grasses such as cereal rye, plants can go from the late vegetative stage to fully-flowered in less than two weeks. Conversely, some perennial grasses like indiangrass can go from the vegetative stage to the elongation stage, then enter a quiescent phase for several weeks until adequate moisture is available which then moves plants into the flowering stages to complete the seed production process.

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 specific stage of development in the plant's life cycle. Physiologic responses to defoliation and subsequent growth potential are affected by growth stage and strongly influence subsequent developmental morphology (Parsons 1988; Brueland et al. 2003).

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 based on plant development (Frank et al. 1993; Brueland et al. 2003).

This chapter addresses the initiation, expansion, and maturation of leaves, stems, and roots and how they regulate the transition from vegetative to reproductive growth and subsequent production of reproductive tissues. The interaction of these processes has profound effects on forage yield, quality, and stand longevity. Emphasis is given to the interactions of developmental morphology on these processes. The authors thank Dr. Howard Skinner for his work on the previous edition of this chapter.

Growth and Development of Plant Organs

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

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Development of Leaf Structures

Production of leaf tissue requires the initiation, elongation, and maturation of new cells. Leaf development has been 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 a 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 (Figure 7.1).

The cell division zone is at the very base of the leaf, 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 2–3 mm of the elongating leaf (Skinner and Nelson 1995), whereas mesophyll cell division continues throughout the basal 10–15 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 100–1000 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 related to leaf elongation rate.

Both cell division and elongation of grasses are affected by the environmental and management factors that alter leaf elongation. Thus, defoliation (Schaufele and Schnyder 2000), **hypoxia** (Smit et al. 1989), water deficits (Lecoeur et al. 1995; Granier and Tardieu 1999), and N 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 is a three-phase process (Granier and Tardieu 1999). During the first phase, leaf area and cell number increase in tandem like 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, providing some protection against removal by grazing as well as buffering against adverse environmental conditions. In contrast, elongating forb leaves are exposed to environmental stress (Radin 1983). Thus, forb defoliation by grazers is

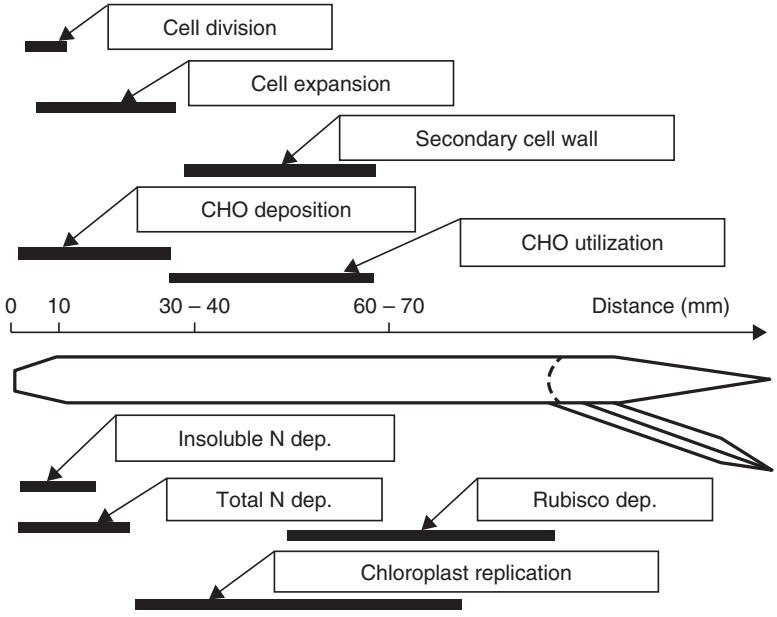

Fig. 7.1. Growth zones and zones of carbon and nitrogen deposition and utilization of elongating tall fescue leaf blades. *Source:* From Skinner and Nelson (1995).

more likely to remove all rapidly expanding leaf material, requiring regrowth to be initiated from new buds or undeveloped leaves. Grazing or mechanical harvest of grass leaves tends to remove 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 (DM) accumulation (Figure 7.2). 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 300–400 $mg\,g^{-1}$ 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 DM in the cell division zone.

As with C 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% 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 C 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 DM 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 C sink to a C source for the rest of the leaf. Similarly, as leaf development continues, the leaf 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 30–60% 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 C 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 in forbs. For example, 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 blade development happens in relative darkness within the whorl of mature sheaths, whereas all stages of forb leaf development occur in full light exposure.

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). Increased elongation occurs at the same time DM and carbohydrate concentrations in the growth zone decrease (De Visser et 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 C balance for the plant. Similarly, narrow and thin leaves occur at low irradiance, allowing increased leaf elongation to occur, despite reduced DM import into the elongation zone (Schnyder and Nelson 1989; Sanderson

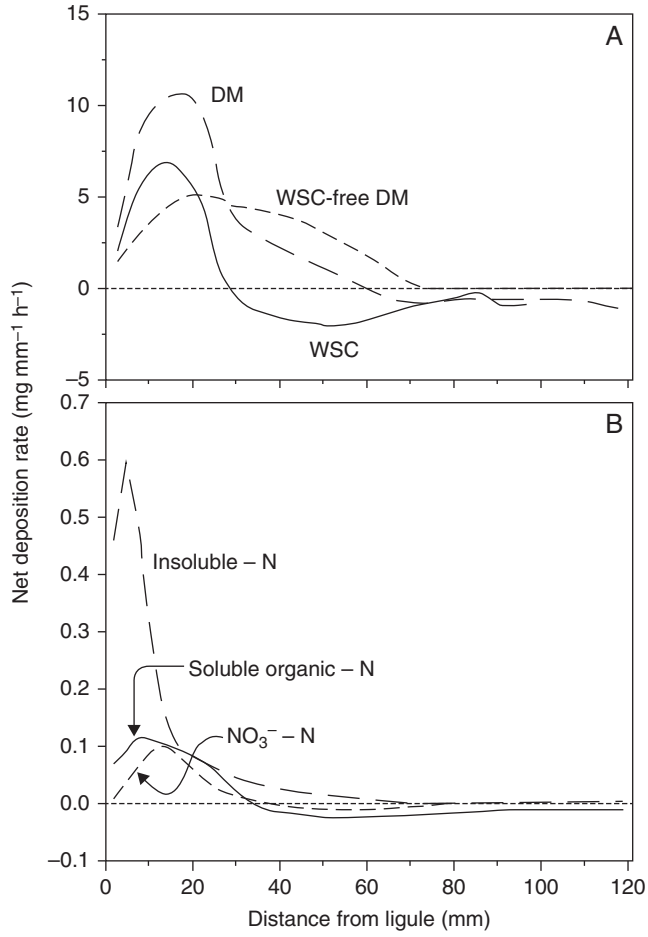

Fig. 7.2. Zones of net deposition and depletion for dry matter (DM), water-soluble carbohydrates (WSC), water-soluble carbohydrate-free dry matter (WSC-free DM), insoluble-N (polypeptides and nucleic acids), soluble organic-N (free amino acids, nucleic acids, and small peptides), and NO_3^--N in elongating tall fescue leaves. The sheath of the previous leaf would enclose the basal 100 mm. *Source:* Adapted from Allard and Nelson (1991) and Gastal and Nelson (1994).

and Nelson 1995). Leaves of forbs also 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), but the effect on leaf thickness was not reported.

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 internodes remain relatively short during vegetative growth but elongate 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 7.1). 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 7.1).

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) reported tiller buds can develop in the axil of the prophyll, a small scaly leaf at the base of each tiller.

When prophyll tillers are accounted for, 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 a 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 (Figure 7.3). 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 becoming 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).

Table 7.1 Synchronization of major developmental transitions involving epidermal cell division and elongation during initiation and appearance of tall fescue leaves and tillers

Haun index	Node	Event	Haun index	Node	Event
1.9	4	Division ends in sheath of leaf 2	2.8	5	Division ends in sheath of leaf 3
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).

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.

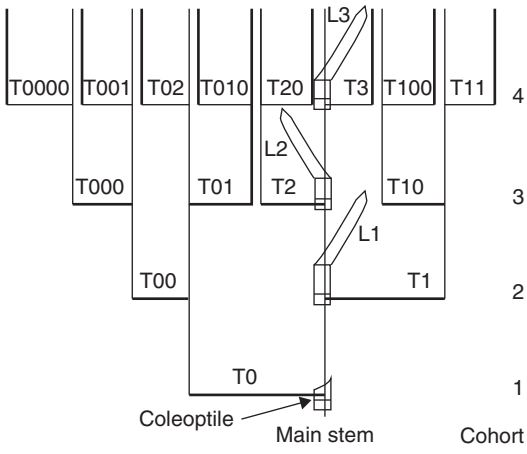

Fig. 7.3. Appearances of tiller cohorts are synchronized with leaf appearance on the main stem (MS). Tillers (T) are named for the leaf axil in which they appear; T0 appears in the axil of the **coleoptile** and tillers; T×0 appears in the prophyll axil of each tiller. Tillers within a cohort that emerge do so at almost the same time, usually within 0.6–1.0 phyllochron after appearance of the main-stem leaf that is two phytomers younger than the tiller, i.e. T1 appears after appearance of L3. *Source:* Adapted from Skinner and Nelson (1992).

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 morphologic stages. First, a seminal taproot develops after establishment and is followed by stolon growth to form a dispersed clonal stage one to two years later (Brock et al. 2000). Death of the taproot and primary stolon initiates the fragmentation of the parent plant into numerous 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 Developmental Morphology

Developmental morphology refers to the series of changes in structure and arrangement of plant components associated with plant maturity (Esau 1960). Developmental morphology is similar among grass species with only minor variations separating growth forms (Briske 1991). Temperature and photoperiod are important in controlling the rate of plant morphologic development (Briske 1991; Gillen and Ewing 1992). Developmental morphology within a species has been reported to have strong linear relationships to accumulated growing degree days (GDD) and day of the year (Kalu and Fick 1981; Buxton and Marten 1989; Hendrickson 1992). The relationship between developmental morphology and day of the year can be partially attributed to the process of floral **induction** which occurs in response to photoperiodic stimulus (Briske 1991). Many plant species have photoperiod requirements for floral induction (Salisbury and Ross 1985). Smooth bromegrass is photoperiod sensitive and requires a primary floral induction period of short days and a secondary period of long days and is, therefore, classified as a short-**long-day plant** (Heide 1984). Other perennial, cool-season grasses, such as intermediate wheatgrass are photoperiod sensitive and have a dual induction requirement for flowering (Heide 1994). Switchgrass and big bluestem are photoperiod sensitive and require short days for floral induction (Benedict 1941). Vegetative growth of smooth bromegrass, intermediate wheatgrass, switchgrass, and big bluestem terminates with inflorescence development and is, therefore, determinate in growth habit (Dahl and Hyder 1977). Following floral **induction**, the grass tillers advance to the seed-ripening stages, growth stops, and tiller senescence occurs.

The architectural organization, palatability and accessibility to herbivores, and regrowth potential following defoliation are determined by the developmental morphology of plants (Briske 1991). Production practices such as grazing management, cutting, and seed production should be based on an accurate assessment of developmental stage (Moore et al. 1991). 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.

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 7.2). 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.

Table 7.2 Morphologic 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
Post-ripe seed	Seed post-ripe; 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 pre-bud)	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).

Quantifying Developmental Morphology

Numerous systems have been developed to accurately quantify the growth and development of plants (Vanderlip 1972; Haun 1973; Zadoks et al. 1974; Fehr and Caviness 1977; Kalu and Fick 1981; Simon and Park 1983; Moore et al. 1991; Sanderson 1992). Many of these systems were intraspecific or difficult to apply in the field. For example, the soybean staging system described by Fehr and Caviness (1977) described at least five vegetative stages and eight reproductive stages and the reproductive stages varied between determinate and indeterminate cultivars. Kalu and Fick (1981) presented a staging system for alfalfa which included ten growth stages ranging from early vegetative to ripe seed pod. This system included two methods to quantify morphologic stage of alfalfa shoot populations based on mean stage by count (MSC) and mean stage by weight (MSW).

In grasses, Phillips et al. (1954) used six general stages ranging from vegetative stage to seeds at **dough stage**. The vegetative stage included a broad spectrum of tillers which ranged from early elongation to the **boot stage** and lacked identification of non-elongated tillers. Haun (1973) developed a system for quantifying wheat development which integrated the number of leaves developed and the rate of development of the next older plant part into plant development. Simon and Park (1983) modified an earlier system developed by Zadoks et al. (1974) which included eight primary growth stages subdivided into secondary stages. They noted the variability of growth stages in cross-pollinated forage grasses was much larger than in cultivars of self-pollinated cereals. This system was applicable to most grass species but is complex and difficult to apply under field conditions (Moore et al. 1991).

The comprehensive growth-staging system developed by Moore et al. (1991) is applicable to most annual and perennial grasses, is easily applied in the field, and produced repeatable results (Hendrickson 1992). This comprehensive growth-staging system contains four primary-growth stages for quantifying the developmental morphology of established perennial grasses: vegetative, elongation, reproductive, and seed ripening (Moore et al. 1991). Secondary stages within each primary stage describe specific events and are given numerical indices to quantify tiller population development. A representative sample of tillers is collected from the **sward** to determine the mean growth index for the tiller population based on MSC or MSW (Kalu and Fick 1981). The system can be used to quantify the relationship between developmental morphology and forage quality of the population (Mitchell et al. 2001).

The systems developed to describe and quantify morphologic development of forage species share some common characteristics, including a defined series of morphologic 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 phenologic relationships are useful for timing management practices that depend on maturity.

Attempts to develop a universal system for describing and quantifying morphologic development of forage crops has 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 growth-staging systems specific to individual crops, including forages (Table 7.3).

Table 7.3 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).

Alfalfa

The recommended system for staging alfalfa was originally developed by Kalu and Fick (1981) and was later modified by Fick and Mueller (1989). It recognizes ten stages of development that occur within four growth phases (Table 7.4). 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 morphologic descriptors are specific to alfalfa but can be modified for other species. However, they are not generally 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 7.4) 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 morphologic descriptors. It performed well. The ten-stage systems for both alfalfa and red clover include length descriptors that are not strictly morphologic (Fick and Mueller 1989). Stem length varies among cultivars of both species, so vegetative stages 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 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 is assigned an index of 3.5. The Haun system applies only to leaf development through stem elongation, so its use is primarily limited to vegetative growth. It has been used to predict grazing readiness of native and introduced pastures (Frank et al. 1993).

Table 7.4 Developmental stages, numerical indices, and morphologic 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).

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: (i) vegetative, (ii) elongation, (iii) reproductive, and (iv) seed ripening (Table 7.5). Within each primary stage, substages are defined that correspond to specific morphologic 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 morphologic events (*N*) that occur for that species or environment. The reproductive and seed-ripening primary stages each have six secondary or substages, 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

Table 7.5 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	$(n/N) + 0.9$	*N*th 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	$(n/N) + 1.9$	*N*th 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.

morphologic 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 morphologic 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, though the coding of the numerical index to descriptors varies among systems.

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 (Sanderson 1992; Brueland et al. 2003). The goal is simply to provide a clear account of the maturity of the forage in relation to other factors of interest.

A potentially more powerful use of numeric indices is developing phenologic models for predicting forage development. Such models relate developmental morphology to climatic variables, such as photoperiod and accumulated heat units. Development of robust phenologic models would enable forage producers to predict the occurrence of important morphologic 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 morphologic 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 (DOY) and GDDs. 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 morphologic

development (Mitchell and Moser 2000). In contrast, big bluestem development was more accurately predicted ($r^2 = 0.83$) using a nonlinear equation based on GDDs, 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). Prediction equations for MSC and MSW were developed based on DOY and GDD. The equations were subsequently validated over two additional growing seasons in Nebraska and Kansas (Figure 7.4). Switchgrass and big bluestem MSC and MSW were related linearly in all environments. Linear DOY calibration equations accounted for 96% of the variation in switchgrass MSC across four environments, which indicates that switchgrass development was related to photoperiod and that general management recommendations could be based on DOY in the central Great Plains. Quadratic GDD calibration equations accounted for 83% of the variation in big bluestem MSC across four environments, which indicates that big bluestem development is more difficult to predict and management recommendations in the central Great Plains should be based on morphologic development which is best predicted by GDD. 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. Developing similar equations for important forage species, within different regions, could be of great benefit to producers.

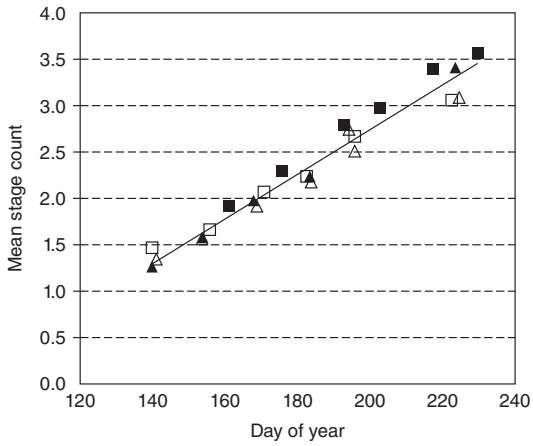

Fig. 7.4. Actual and predicted mean stage count of 'Trailblazer' switchgrass grown in Kansas (■) and Nebraska (Δ) during 1992 (*open symbols*) and 1993 (*closed symbols*). Predicted MSC = 0.024(Day) – 2.063. *Source:* Adapted from Mitchell et al. (1997).

Plant Maturity and Relationships to Forage Quality

Quantifying maturity of perennial grass tiller populations is essential to characterize nutrient content throughout the developmental cycle. As plant maturity increases, the quality for ruminant animals decreases because of an increase in cell wall concentration and decrease in crude protein (CP) concentration. Quantifying the growth and development of forage grasses and determining relationships with forage quality is essential for making forage management decisions.

Forage quality is affected by genetic, physiologic, environmental, and plant developmental factors (Van Soest 1982). The influences of these factors on forage quality are highly integrated and often difficult to isolate. Plant maturity is the major factor affecting developmental morphology and forage quality (Nelson and Moser 1994). The existence of relationships between plant maturity and forage quality of perennial grasses has long been recognized (Phillips et al. 1954). However, the environment can modify the impact of plant maturity on forage quality (Buxton and Fales 1994). Factors such as high temperature, high-solar irradiation, and abundant water may accelerate the maturation process, while factors such as clipping, grazing, and disease may retard the maturation process (Van Soest 1982).

Environmental factors that affect plant growth have a profound effect on forage quality (Van Soest 1985). High temperatures reduce forage quality at similar physiologic ages (Wilson 1983), possibly through decreases in leaf: stem ratios with high temperatures promoting stem growth over leaf growth (Buxton and Fales 1994). Metabolic activity increases as temperature increases which results in higher accumulations of cellulose, hemicellulose, and lignin, while forages grown in cooler climates have higher carbohydrate reserves and protein concentrations associated with needs to develop winter-hardiness (Van Soest 1985). Cell-wall materials deposited at lower temperatures are less lignified and more digestible (Nelson and Moser 1994).

Increasing irradiation stimulates photosynthetic activity which promotes synthesis of soluble sugars and starches which dilute cell-wall material (Buxton and Casler 1993). High irradiance or extended photoperiods for short timeframes generally increases forage quality (Buxton and Casler 1993). Prolonged periods of shade may reduce photosynthate availability which reduces secondary cell wall deposition, resulting in lower lignin concentrations (Buxton and Casler 1993).

The effect of water on forage quality is variable. If water is limiting, plant advancement toward maturity may be hindered, resulting in higher forage quality. Mild water stress increases forage quality by increasing leaf: stem ratios and increasing the digestibility of leaves and stems (Nelson and Moser 1994). However, if water stress is too severe, perennial plants may go dormant and translocate reserves into the roots and crown, reducing the forage quality of the plant (Van Soest 1985).

Factors influencing plant maturity may be site specific (weather, water, and management) or vary on a geographic basis (light quality, light quantity, soil, and climate) (Van Soest 1982). Therefore, quantifying relationships between developmental morphology and forage quality in different environments is necessary to provide information for developing strategies for improving utilization and seasonal distribution of perennial forage grasses.

Factors that influence forage quality are complex and interactive (Van Soest 1982; Akin 1989). The anatomic organization of C_4 grasses causes forage quality to be lower than for C_3 grasses (Akin 1989). The loose arrangement of mesophyll cells in C_3 grasses increases intercellular air space allowing more rapid penetration by rumen bacteria into the leaf, increasing digestion (Hanna et al. 1973). Cool-season species typically accumulate more **total nonstructural carbohydrates (TNC)** in the form of fructan than warm-season species, particularly at low temperatures, which greatly improves the quality of cool-season species (Nelson and Moser 1994). However, plant maturity is the major factor determining forage quality within a species (Nelson and Moser 1994). As plant maturity increases, forage quality for ruminant animals decreases through an increase in cell-wall concentration and a decrease in crude protein concentration (CP). The decline in forage quality associated with increased maturity may be partially explained by a decrease in leaf material and an increase in stem material. Stem elongation and inflorescence development form lower quality stem material that dilutes the higher quality leaf material (Nelson and Moser 1994).

Griffin and Jung (1983) reported the percentage of total DM production of leaf tissue of switchgrass declined from 71% to 31% and big bluestem declined from 64% to 21% as maturity progressed. With advancing maturity, stems decreased in quality faster than leaves (Griffin and Jung 1983; Nelson and Moser 1994). The lower forage quality of grass stems compared to grass leaves can be attributed to differences in anatomic characteristics of grass leaves and stems. Grass stems are composed of an epidermis covered with a thick waxy cuticle which is nearly impervious to microbial penetration (Monson et al. 1972), plus more sclerenchyma and parenchyma tissue, resulting in a more rigid, less digestible tissue than leaves (Akin 1989).

Dry Matter Digestibility

The ***in vitro*** procedure for estimating DM digestibility (Tilley and Terry 1963), later modified with direct acidification by Marten and Barnes (1980), has allowed researchers to rapidly quantify the digestibility of large numbers of forage species (Vogel et al. 1981). *In vitro* DM disappearance (IVDMD) of perennial forage grasses declined as the growing season progressed and maturity advanced (Anderson and Matches 1983; Jung and Vogel 1986; Sanderson and Wedin 1989; Mitchell et al. 1994). Cool-season grass species tended to be higher in IVDMD than warm-season grass species at similar maturities (Akin 1989). Vascular bundles of leaves of C_4 grasses are closely spaced and surrounded by a thick-walled parenchyma bundle sheath, whereas vascular bundles of C_3 grasses are widely spaced with less distinct parenchyma bundle sheaths and loosely arranged mesophyll cells which are rapidly digested (Buxton and Casler 1993).

The IVDMD concentrations of smooth bromegrass and timothy leaf blades, stems, and herbage declined linearly with increasing maturity (Sanderson and Wedin 1989). Maturity accounted for more IVDMD variation in timothy leaf blades and herbage than in bromegrass. The IVDMD of the stems of both smooth bromegrass and timothy declined more rapidly than did the IVDMD of the leaf blades of each species. The IVDMD of smooth bromegrass herbage ranged from approximately 500–750 g kg^{-1}.

There was a linear decline in IVDMD of two cultivars each of orchardgrass, smooth bromegrass, reed canarygrass, and tall fescue as maturity advanced (Buxton and Marten 1989). Total herbage IVDMD of the two smooth bromegrass cultivars harvested between 10 May and 5 July ranged from approximately 440–780 g kg^{-1}. With four grass species, the top leaf blades were most digestible, the inflorescences were intermediate, and the stems were least digestible (Buxton and Marten 1989). Day of the year, GDD, and morphologic stage accounted for at least 95%, 92%, and 89%, respectively, of the variation associated with IVDMD for all species during the two-years study.

Similar decreases in warm-season grass IVDMD with advancing maturity have been observed. The nutritional value of perennial warm-season grasses is primarily limited by digestible energy (Moore et al. 1993). The IVDMD of switchgrass leaves declined linearly throughout the growing season (Anderson 1985). The whole-plant IVDMD declined approximately 20 g kg^{-1} per week as switchgrass and caucasian bluestem matured from the vegetative to the **heading** stages (Anderson and Matches 1983). They also noted that switchgrass whole-plant IVDMD was higher than caucasian bluestem IVDMD at similar growth stages, but the IVDMD of the two species was nearly equal on a given date (Anderson and Matches 1983). Balasko et al. (1984) reported switchgrass

IVDMD declined with maturity with IVDMD at the **boot stage** ranging between 504 and 576 g kg^{-1}.

Switchgrass and big bluestem leaf and stem IVDMD declined throughout the growing season, and IVDMD was higher during a dry year than during a year with above normal precipitation (Perry and Baltensperger 1979). Switchgrass IVDMD was usually higher than big bluestem IVDMD when harvested on a common day of the year, and stage of maturity had more influence on IVDMD than did unfavorable precipitation (George and Hall 1983). The IVDMD of big bluestem harvested from tallgrass prairies declined as the growing season progressed and ranged from 710 to 508 g kg^{-1} in mid-June and mid-August, respectively (Mitchell et al. 1994). The highest IVDMD of 20 elite switchgrass populations ranged from 650 g kg^{-1} in vegetative growth stages to 492 g kg^{-1} at heading (Hopkins et al. 1995). Switchgrass IVDMD was best predicted by GDD which accounted for 86% of the variation, whereas big bluestem IVDMD was best predicted by MSW which accounted for 90% of the variation (Mitchell et al. 2001).

Fiber Concentration

Warm-season grasses tend to have higher fiber concentrations than cool-season grasses at similar maturities (Griffin et al. 1980; Jung and Vogel 1986). Increased fiber concentrations in perennial warm-season grasses would result in lower digestibility and reduced intake (Kilcher 1981).

Eight species of cool-season grasses increased in lignin and **crude fiber** up to the flowering stage and, in some species, to the seed-dough stage (Phillips et al. 1954). They concluded on the basis of the changes in lignin and crude fiber concentration that lignin was preferred over crude fiber as a criterion for **feeding value** (Phillips et al. 1954).

Neutral detergent fiber concentrations (NDF) of switchgrass and big bluestem leaves changed little with advanced maturity (Griffin and Jung 1983). However, NDF accumulation in the stem tissue of switchgrass and big bluestem increased rapidly with maturation. Switchgrass leaves and stems averaged 23 and 49 g kg^{-1} higher NDF than big bluestem leaves and stems, respectively, at early head emergence. Lignin concentrations in switchgrass and big bluestem leaves and stems increased with maturity. However, lignin concentrations in the stems increased at a much faster rate than lignin concentrations in the leaves. At early head emergence, lignin concentrations for switchgrass leaves and stems was 47 and 83 g kg^{-1}, respectively, whereas lignin concentrations for big bluestem leaves and stems were 46 and 61 g kg^{-1}, respectively. However, lignin continued to accumulate in big bluestem after seedheads emerged, indicating the importance of harvesting prior to heading.

The NDF, acid detergent fiber (ADF), and lignin concentrations increased more than three times faster in switchgrass stems than in the leaves during the first 25 days of stem collection (Anderson 1985). At similar growth stages, leaves that developed early in the growing season contained less NDF and ADF than leaves that developed late in the growing season. Switchgrass leaves never contained less than 600 g kg^{-1} NDF, and average NDF increased 0.13 g kg^{-1} d^{-1} from the two-leaf stage in May until late July, whereas ADF concentration increased less consistently. Lignin concentrations ranged from 21 to 128 g kg^{-1} in leaves and from 58 to 152 g kg^{-1} in stems and was consistently low in leaves in the whorl (Anderson 1985).

Hendrickson (1992) reported the NDF and ADF concentrations of prairie sandreed and sand bluestem leaves did not vary in response to morphologic advancement as measured by MSC or MSW. Prairie sandreed leaf NDF was higher than sand bluestem leaf NDF, but leaf ADF of the two species was similar throughout the growing season. Neither MSC nor MSW had consistently high correlation coefficients with NDF and ADF concentrations. Leaf lignin was highly variable and neither MSC nor MSW had a consistently good relationship with leaf lignin. He concluded the stable leaf NDF and ADF concentrations of both species indicated a decline in cell-wall digestibility rather than a decrease in cell contents was responsible for declines in digestibility.

Switchgrass NDF was best predicted by MSC and MSW (Mitchell et al. 2001). Mean stage weight accounted for 74% of the variability in big bluestem NDF. The model adequately predicted forage quality due primarily to the determinate growth habit of these species. Morphologic development accurately predicted forage quality in many instances.

Crude Protein Concentration

CP concentration of perennial forage grasses typically decreased as maturity progressed (Kamstra 1973; Perry and Baltensperger 1979; Griffin and Jung 1983; Mitchell et al. 1994), and was higher for cool-season grasses than for warm-season grasses at similar growth stages (Kamstra 1973; Griffin et al. 1980). Kamstra (1973) reported that the CP of two cool-season and two warm-season grasses decreased with maturity. The CP of western wheatgrass declined linearly as maturity progressed and ranged from approximately 120–69 g kg^{-1}. Kilcher and Troelsen (1973) reported smooth bromegrass CP ranged from 250 g kg^{-1} in the very immature stage to 80 g kg^{-1} in the mature stage. Perry and Baltensperger (1979) concluded leaf maturation was primarily responsible for declining CP rather than plant development. Griffin and Jung (1983) concluded quality of leaf tissue was responsible for the declining whole-plant forage quality of switchgrass and big bluestem.

Rehm et al. (1971) evaluated the influence of nine fertility levels on smooth bromegrass CP. Smooth bromegrass whole-plant CP ranged from 87 to 240 g

kg^{-1} when harvested at the early inflorescence growth stages. They concluded that CP generally increased with increasing rates of N. Residual effects of yearly N applications had no effect on smooth bromegrass CP.

Newell and Moline (1978) evaluated the CP trends of intermediate wheatgrass throughout the growing season. The CP of intermediate wheatgrass was 297 g kg^{-1} in the very early vegetative growth and continued through the summer with averages well above 100 g kg^{-1}. The extended day-length and high temperatures of the summer were responsible for the low summer CP. Intermediate wheatgrass CP increased with shorter days and cooler night temperatures to 170 g kg^{-1} in mid-August and reached 220 g kg^{-1} in early October from samples taken above 20 cm.

The CP declined in two cultivars each of orchardgrass, smooth bromegrass, reed canarygrass, and tall fescue as maturity advanced (Buxton and Marten 1989). The CP was consistently greatest in reed canarygrass and least in tall fescue. Total herbage CP of the two smooth bromegrass cultivars harvested between 10 May and 5 July ranged from 77 to 314 g kg^{-1}, respectively. The CP in all four species was greatest in the top leaves, intermediate in the inflorescences, and least in the bottom leaves (Buxton and Marten 1989). They concluded that CP was closely related to day of the year, GDD, and morphologic stage. Day of the year, GDD, and growth stage accounted for at least 88%, 77%, and 74%, respectively, of the variation associated with CP during the two-year study.

Switchgrass and big bluestem leaf CP decreased with plant maturation an average of 7 and 11 g kg^{-1} between harvests conducted at 14-day intervals (Perry and Baltensperger 1979). Switchgrass leaf CP was higher than big bluestem on common days of the year, except on the first harvest date when big bluestem leaf CP was highest. Big bluestem leaf CP declined more than switchgrass throughout all harvests. They concluded the decline in CP of forage topgrowth was apparently associated with both leaf maturation and increased stem growth.

Switchgrass and big bluestem leaf CP decreased with plant maturation on average of 15 g kg^{-1} between weekly harvests (Griffin and Jung 1983). Switchgrass averaged 17 g kg^{-1} lower in CP than big bluestem on common days of the year, but big bluestem stem CP declined more rapidly than switchgrass with increased maturity. At early head emergence, switchgrass leaf and stem CP averaged 85 and 38 g kg^{-1}, respectively, whereas big bluestem leaf and stem CP averaged 108 and 48 g kg^{-1}, respectively. The CP of switchgrass leaves declined as maturity progressed and the decline was most rapid between a leaf's emergence in the whorl until collaring of the following leaf (Anderson 1985). The decline in CP of the stems was more rapid than in most leaves. Switchgrass and big bluestem CP were best predicted by GDD which accounted for 91% and 90% of the variation in CP, respectively (Mitchell et al. 2001). Although no universal parameter adequately predicted concentrations of IVDDM, CP, and NDF, it was possible to accurately predict quality with readily available environmental data and measures of plant maturity (Mitchell et al. 2001).

Rumen Undegradable Protein

CP concentration alone may not be adequate to identify dietary protein for nutritional purposes (Mangan 1982). Dietary protein consumed by ruminant animals is degraded by microbial fermentation in the rumen or "escapes" to the small intestine. Protein protected from ruminal degradation allows more amino acids to reach the small intestine, increasing animal performance (Chalupa 1975). The rumen degradability of forage protein is highly variable among forage species (Petit and Tremblay 1992) and varies with maturity (Mullahey et al. 1992).

Rumen degradable protein (RDP) is highly variable between species harvested at similar stages of developmental morphology. Warm-season grasses tend to degrade more slowly in the rumen than cool-season grasses (Akin 1989). Anatomic differences between C_3 and C_4 grasses may explain some of the variability in ruminal protein degradation (Mullahey et al. 1992). Whole-plant rumen undegradable protein (RUP) was greater in switchgrass than smooth bromegrass, except at the last harvest when RUP was similar in both species (Mullahey et al. 1992). The RUP for switchgrass ranged from 52 to 18 g kg^{-1} DM and declined with maturity. The RUP for smooth bromegrass ranged from 28 to 18 g kg^{-1} DM and was lowest for the most immature growth stage. They attributed the differences in ruminal protein degradation between switchgrass (C_4) and smooth bromegrass (C_3) to anatomic differences. RUP for switchgrass leaves was greater than stems at each harvest date, and both leaf and stem **escape protein** decreased linearly with advancing maturity (Mullahey et al. 1992). **Escape protein** of smooth bromegrass was consistently greater in leaves than stems. Greater RUP occurred at later harvests for smooth bromegrass leaves but occurred early in the growing season for stems. Changes in the leaf-stem ratio had a significant impact on whole-plant RUP (Mullahey et al. 1992).

Hoffman et al. (1993) evaluated the influence of maturity on ruminal DM and CP degradation of three legume species and five cool-season grass species. They reported that legumes exhibited more extensive ruminal DM degradation than did grasses, and mature grasses were lowest in RDP. Smooth bromegrass ruminal DM degradation was 620 g kg^{-1} at emergence of the second node, 555 g kg^{-1} at the **boot stage**, and 410 g kg^{-1} at full heading (Hoffman et al. 1993). Smooth bromegrass ruminal CP degradation was 760 g kg^{-1} at emergence of the second node, 720 g kg^{-1} at the boot stage, and 644 g kg^{-1} at full **heading** (Hoffman et al. 1993). They concluded

the relative relationship and range among forage species and maturities should be of primary interest.

Mitchell et al. (1997) quantified the relationships between the morphologic development and RDP, RUP, and microbial protein of intermediate wheatgrass, smooth bromegrass, switchgrass, and big bluestem. The mean stage of cool-season grasses was higher than that of warm-season grasses throughout the growing season. The RDP decreased as plant maturity increased for all species. The RUP expressed as a percentage of CP for the cool-season grasses was lower than that for warm-season grasses. The RUP for intermediate wheatgrass, smooth bromegrass, and switchgrass remained constant across maturities, but RUP for big bluestem decreased as maturity increased. Microbial augmentation of RUP decreased as CP decreased in all species. The RUP corrected for acid detergent insoluble N and microbial protein was relatively constant across plant maturities. Quantifying RUP across a range of plant maturities provides a starting point for incorporating RUP of forage grasses into animal diets.

Canopy Architecture and Tiller Demographics

Canopy architecture influences many plant canopy processes and must be considered when describing the interaction between plants and the environment (Welles and Norman 1991; Redfearn et al. 1997). Canopy architecture affects forage plant physiology, quality of forage offered to grazing animals, and animal grazing patterns (Nelson and Moser 1994). Canopy architectural measurements such as leaf area index (LAI) and mean leaf inclination angle (Welles and Norman 1991) can be related to relative light interception, forage productivity, forage availability, and forage accessibility to grazing livestock (Redfearn et al. 1997).

The phytomer is the basic modular unit of growth in grass plants and consists of a leaf blade, leaf sheath, node, internode, and axillary bud (Hyder 1972; Briske 1991). A series of phytomers forms the grass tiller, which consists of a single growing point, a stem, leaves, roots, nodes, dormant buds, and if reproductive, a potential inflorescence (Hyder 1972; Vallentine 1990). Grass tillers are further organized into anatomically attached groups which form the grass plant (Vallentine 1990; Walton 1983). Grass plants collectively form a sward.

A grass leaf is composed of a sheath and blade. New leaves are generated by cell division and pushed upward by expansion at the basal meristem which results in the linear aspect of the entire leaf (Mauseth 1988). Leaf blades emerge through the whorl and extend to the top of the canopy in vegetative grass canopies (Allard et al. 1991). The oldest leaves of a grass tiller have the lowest level of insertion from the plant base, while new leaves have a higher insertion level on the plant (Wilson 1976; Walton 1983). Leaf length in grass species is controlled by the transport limitations of the vascular bundles (Mauseth 1988). In green panic, leaf length and area increased progressively up to leaf 10, then decreased to the **flag leaf** (Wilson 1976). Leaves of high-insertion levels developed more slowly, stayed green longer, and senesced more slowly than those of a low-insertion level (Wilson 1976). When corn leaves reach a predetermined length, the basal meristem disorganizes, and leaf growth stops (Mauseth 1988).

Grasses are efficient forage producers because of the location of the meristematic tissue, growth habits of the plant, and the ability of the plant to tiller (Rechenthin 1956). The number of live tillers within a plant or per unit area is determined by the seasonality of tiller recruitment in relation to tiller longevity (Briske 1991). Tiller density is controlled by the recruitment rate of new tillers, the mortality of existing tillers, and the interaction of recruitment and mortality (Langer et al. 1964; Briske 1991). In a smooth bromegrass sward, tiller density was highest in early spring and decreased as spring growth progressed (Krause and Moser 1980). The reduction in tiller density resulted from the lack of light penetration through the canopy to the depth of the small tillers which caused many of the small tillers to cease functioning and the number of functional tillers to decline (Krause and Moser 1980). However, tiller recruitment in perennial cool-season grasses like smooth bromegrass typically involves at least two tiller generations annually, with tillering episodes occurring in the early spring and a more active tillering episode immediately following **anthesis** (Lamp 1952; Krause and Moser 1980).

Numerical indices are useful for describing the demography of forage populations (Mitchell et al. 1998). This is important because there is often 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. 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 morphologic 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 tiller 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 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 is 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 tiller population maturity for intermediate wheatgrass and big bluestem in mid-June near Mead, NE, and staged using the Nebraska system (Table 7.5). The four vegetative stages, V1, V2, V3, and V4, for big bluestem coded numerically as 1.15, 1.40, 1.65, and 1.9 (Figure 7.5). 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 (Figure 7.6) shows the change in number of tillers in each primary growth stage with respect to time. At the first four sampling dates,

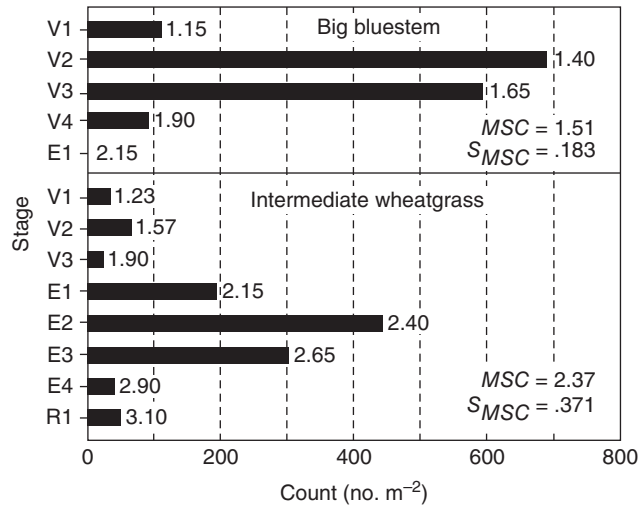

Fig. 7.5. Frequency distribution of tiller growth stages for big bluestem and intermediate wheatgrass populations sampled in mid-June near Mead, NE. *Source:* From Moore and Moser (1995).

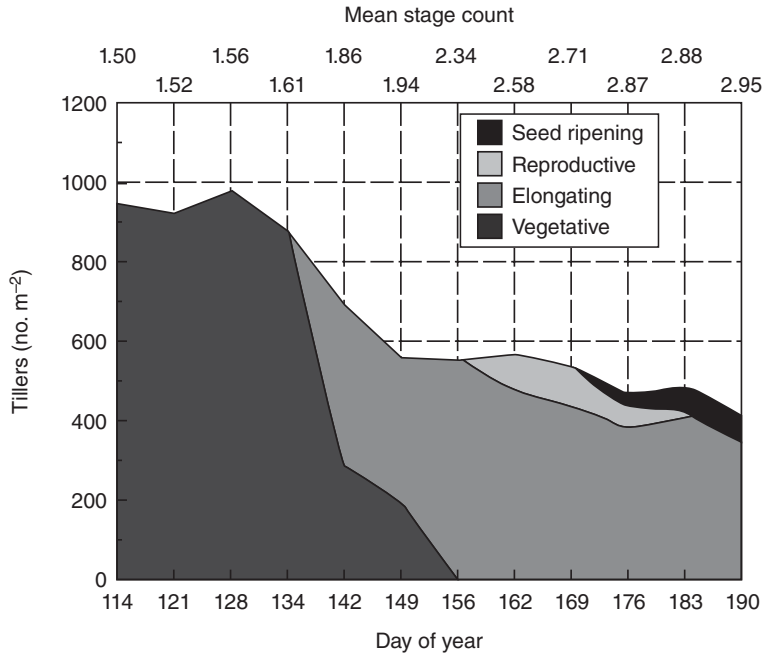

Fig. 7.6. Developmental morphology and demography of an intermediate wheatgrass tiller population during the 1991 growing season near Mead, NE. *Source:* From Moore and Moser (1995).

all tillers were vegetative. In a period of one week, however, over half the tillers began to elongate and in another three to four weeks, some tillers were advancing into reproductive stages. Coincident with the onset of elongation was an increase in tiller mortality that resulted in an almost 40% decrease in tiller density by day 149.

Interestingly, only a relatively small proportion of tillers advanced through the reproductive to seed-ripening stages (Figure 7.6). This population would have been described as fully headed based on visual observation during the reproductive and seed-ripening phases when, in reality, less 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.

Quantifying tiller population morphology on a unit area basis allows changes in tiller demography to be monitored over time. Tiller density and demographics is highly variable across species, but tiller density in perennial grasses typically declines as MSC advances and the growing season progresses (Moore and Moser 1995; Mitchell et al. 1998). Intermediate wheatgrass tiller density generally declined as MSC increased, but smooth bromegrass tiller density followed no clear patterns with increased MSC. Tiller demographics was highly variable by year for intermediate wheatgrass and smooth bromegrass which indicates grazing management should be based on current tiller populations. Tiller populations with a large proportion of vegetative tillers provide grazing livestock the opportunity to select less mature and higher quality tillers. Vegetative tillers declined most rapidly for smooth bromegrass, followed by intermediate wheatgrass, switchgrass, and big bluestem. Switchgrass and big bluestem tiller density generally declined as MSC increased and demographics were more uniform and predictable across years. Big bluestem tiller mortality averaged as many as 47 tillers m^{-2} d^{-1} for the first four weeks. LAI of intermediate wheatgrass, smooth bromegrass, switchgrass, and big bluestem tiller populations increased as morphology advanced (Mitchell et al. 1998). The LAI for all species increased as MSC increased. Maximum LAI for intermediate wheatgrass, smooth bromegrass, switchgrass, and big bluestem was 4.7, 5.1, 4.9, and 5.8, respectively. Integrating tiller demographics and LAI indicates initial grazing order for a four-species complementary grazing system should be smooth bromegrass in early spring followed by intermediate wheatgrass in about two-weeks, switchgrass in late spring, and big bluestem in early summer.

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