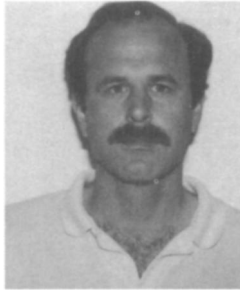


Invited Synthesis Paper

The Editorial Board of the *Journal of Range Management* invited Jeffrey S. Murphy and David D. Briske to prepare this synthesis paper.



Jeffrey S. Murphy received his B.S. in range management from Humboldt State University in 1984 and his M.S. from Utah State University in range science in 1987. He has previously worked as an Extension range technician at Utah State University and as an area Extension agent with Colorado State University. Mr. Murphy is currently completing a Ph.D. program in plant physiology. His dissertation research focuses on the environmental, developmental, and physiological mechanisms that regulate tiller initiation in grasses. Mr. Murphy's research interests include physiological plant ecology, plant population ecology, photobiology and plant-herbivore interactions.



David D. Briske received his B.A. in botany from North Dakota State University in 1973 and his Ph.D. in range science from Colorado State University in 1978. His research and teaching interests include physiological plant ecology, developmental plant morphology, plant-herbivore interactions, clonal plant biology, plant population ecology, and grassland ecology. The goals of Dr. Briske's research program are to develop a greater understanding of the ecophysiology and population ecology of the bunchgrass growth form which dominates rangelands throughout the world and to generate and synthesize ecological information necessary to evaluate current strategies and provide new alternatives for grassland conservation and management.

Regulation of tillering by apical dominance: Chronology, interpretive value, and current perspectives

JEFFREY S. MURPHY AND DAVID D. BRISKE

Authors are Tom Slick graduate research fellow and professor, Dept. of Rangeland Ecology and Management, Texas A&M University, College Station, 77843-2126.

Abstract

The range science profession has traditionally relied upon the concept of apical dominance to explain tiller initiation in perennial grasses. The physiological mechanism of apical dominance is assumed to follow the direct hypothesis of auxin action, which was originally proposed during the 1930's. This hypothesis indicates that the plant hormone auxin (IAA), produced in the apical meristem and young leaves, directly inhibits axillary bud growth. The direct hypothesis was, and continues to be, the sole interpretation

of the physiological mechanism of apical dominance since the concept was initially adopted by the range science profession. However, the direct hypothesis was abandoned by plant physiologists during the 1950's because of experimental and interpretive inconsistencies and the demonstrated involvement of a second hormone, cytokinin, in apical dominance.

The cytokinin deficiency hypothesis has replaced the direct hypothesis as the current hormonally based interpretation of apical dominance. This hypothesis indicates that IAA produced in the apical meristem blocks the synthesis or utilization of cytokinin within axillary buds inhibiting their growth. Despite wide acceptance, numerous issues remain unresolved concerning this hypothesis, suggesting that it may also be an incomplete interpretation of the physiological mechanism of apical dominance.

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The interpretive value of the apical dominance concept is much less consistent than generally assumed. Apical meristem removal does not always promote tiller initiation in grasses and tillering may occur in plants with intact apical meristems. These inconsistencies demonstrate that the apical dominance concept is an overly restrictive interpretation of the regulation of tiller initiation in perennial grasses. Numerous environmental variables including resource availability, radiation quality, and competition are known to exert strong influences on tiller initiation. The extreme spacial and temporal variability of environmental variables and resource distribution on rangelands increases the importance of these variables by potentially overriding or constraining the physiological mechanism(s) regulating tiller initiation.

Physiological explanations of apical dominance are currently inconclusive and the response of tiller initiation to apical meristem removal is inconsistent. Therefore, the range science profession should reevaluate the inordinate emphasis currently placed on the hormonal mechanism of apical dominance as the predominant interpretation for the regulation of tiller initiation in perennial grasses. Alternative interpretations of the regulation of tiller initiation must integrate the contemporary physiological perspective with the effects of environmental variables to more effectively explain the magnitude and timing of tillering in grasses.

Key Words: axillary bud, bud inhibition, correlative inhibition, defoliation, developmental morphology, plant hormones, plant physiology, tiller

The perennation and sustainable productivity of grasses and grasslands are dependent on successive tiller initiation from axillary buds of previous tiller generations. Although perennial bunchgrasses are relatively long-lived (Canfield 1957, Briske 1991), individual tiller longevity does not exceed 2 years in most temperate species (Langer 1956, Robson 1968, Briske 1991). Consequently, tiller initiation must occur annually to offset mortality and maintain plant productivity, size, and competitive ability. Tiller initiation and mortality establish the density of live tillers within species populations, which collectively influence community composition and productivity. Tiller density establishes the basis for potential productivity because it represents the pool of meristematic tissues from which growth may occur. Therefore, insight into the processes regulating tiller initiation are essential for a thorough understanding of grassland ecology and the development of effective management strategies.

The developmental morphology of tiller growth and initiation are qualitatively similar among species within the Poaceae. Individual tillers consist of a series of phytomers differentiated sequentially from a single apical meristem (Etter 1951, Hyder 1972). An individual axillary bud (i.e., rudimentary apical meristem) is differentiated as a component of each phytomer to form the basic structural unit of the tiller (Fig. 1). Cells in the 2 outermost layers of the apical meristem divide to form leaf primordia (i.e., rudimentary leaves) while cell division in the third innermost layer of the apical meristem, on the side opposite each primordium, gives rise to axillary buds (Sharman 1945, Briske 1991). Although axillary buds are differentiated from the apical meristem, they are subordinate to the apical meristem in terms of position and time of development. Once axillary bud differentiation is complete, bud growth may continue giving rise to a new tiller or growth may be arrested (Dahl and Hyder 1977).

Inhibition of axillary bud growth following bud formation is widely assumed to be imposed by the physiological mechanism responsible for apical dominance. Apical dominance refers to the control exerted by the apical portion of the shoot, which includes the apical meristem and young leaves, on axillary bud growth following bud formation (Sachs and Thimann 1967, Cline 1991).

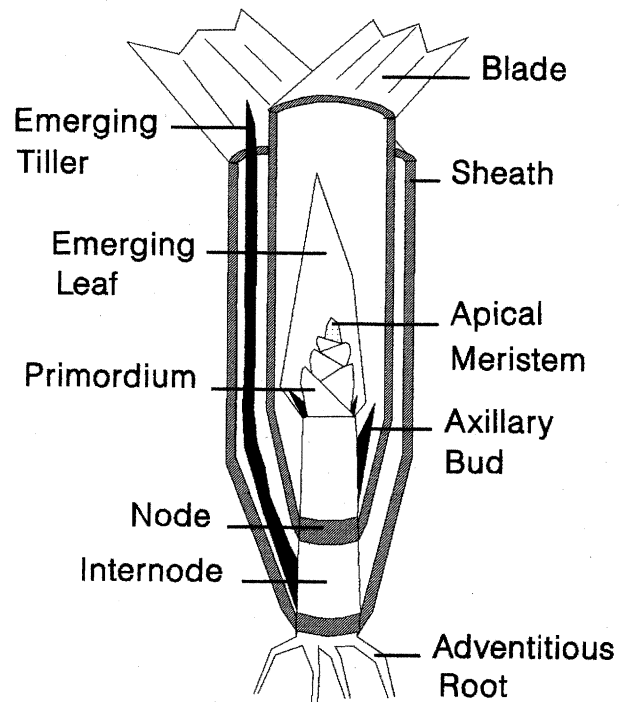


Fig. 1. Tiller in longitudinal view illustrating the apical meristem, components of individual phytomers, and an emerging leaf and tiller. A single axillary bud (rudimentary apical meristem) is differentiated with each phytomer from the apical meristem. It is widely assumed by the range science profession that axillary buds may grow to form tillers if not inhibited by apical dominance. Modified from Etter (1951) and Jewiss (1972).

The term "apical meristem" is used throughout this paper to collectively refer to the apical meristem and associated leaf primordia. The range science profession has traditionally relied upon the apical dominance concept to interpret the timing and magnitude of tiller initiation in grasses. Apical meristem removal by defoliation is assumed to release axillary buds from hormonal inhibition and stimulate tiller initiation.

This paper was developed to review the apical dominance concept as it is currently interpreted and applied to the regulation of tiller initiation within the range science profession. Specific objectives are to (1) develop a brief historical perspective of the physiological mechanisms responsible for apical dominance, (2) document the incorporation of the apical dominance concept into the range science literature, (3) examine the interpretive value of apical dominance in range science and management with specific reference to tiller initiation, and (4) briefly summarize current perspectives of the physiological mechanisms responsible for apical dominance.

Chronology of Apical Dominance Mechanisms

Several excellent reviews have summarized the voluminous research literature addressing the physiological mechanisms of apical dominance which have been investigated since the early 1900's (Went and Thimann 1937; Phillips 1969, 1975; Rubinstein and Nagao 1976; McIntyre 1977; Hillman 1984; Martin 1987; Tamas 1987; Cline 1991). Initial investigations of the physiological mechanisms of apical dominance were conducted exclusively with dicots and this group of plants continues to receive major emphasis. No less than 6 major hypotheses have been advanced since 1900 to explain the inhibition of axillary bud growth by the apical meristem (Table 1). Five of these 6 hypotheses were developed by 1940, 3 years before the first reference to apical dominance appeared in the range science literature (Stoddart and Smith 1943).

Table 1. Chronological summary of the major hypotheses proposed to explain the physiological mechanism responsible for apical dominance. The seminal paper(s) for each hypothesis is referenced.

Hypothesis	Reference	Brief Description
Nutritive	see Went and Thimann (1937) Gregory and Veale (1957) Hillman (1984)	Apical meristems compete with axillary buds for nutrients and water inhibiting their growth.
Inhibitor	Reed and Halma (1919) Harvey (1920) Snow (1925, 1940)	An unidentified translocatable chemical inhibitor produced in the apical meristem directly inhibits axillary bud growth.
Direct	Thimann and Skoog (1933, 1934) Thimann (1937)	IAA produced in the apical meristem is transported to axillary buds and directly inhibits their growth. A later revision stated that bud inhibition resulted from supraoptimal IAA concentrations.
Nutrient diversion	Went (1938, 1939)	Root-produced substances critical for axillary bud growth are preferentially transported to the site of IAA production in the apical meristem. Buds remain inhibited until a sufficient amount of these substances accumulate to promote bud growth.
Vascular connection	Van Overbeek (1938) Sorokin and Thimann (1964)	IAA adheres to the vascular traces of axillary buds blocking the entry of substances required for growth. This was originally termed the "blocking" hypothesis.
Cytokinin deficiency	Wickson and Thimann (1958)	IAA produced in the apical meristem is transported to axillary buds where it prevents cytokinin synthesis or utilization thereby inhibiting bud growth.

The following chronology is intended to summarize what was known about the physiological mechanisms of apical dominance prior to the adoption of the apical dominance concept by the range science profession.

Dicots

It was widely accepted during the late 1800's that the orderly pattern of plant development could be explained on the basis of interactions between individual plant organs. These organs were presumed to be in direct competition for limited supplies of water and nutrients within the plant. This concept of internal competition led to the development of hierarchies of dominance in which the oldest shoot garnered the bulk of available resources at the expense of younger shoots (Went and Thimann 1937, Martin 1987).

The earliest interpretation of physiological mechanism of apical dominance was an extension of the "dominance hierarchy" concept. The apical meristem, as the oldest shoot organ, was assumed to be the strongest sink for water and nutrients within the plant. As the apical meristem monopolized these resources, their availability fell below critical levels required for axillary bud growth (Hillman 1984, Martin 1987). Consequently, axillary bud inhibition was assumed to result from the inability of buds to successfully compete with the apical meristem for limited supplies of water and nutrients within the plant. This interpretation was later termed the "nutritive" hypothesis (Phillips 1969, 1975) and was the first major hypothesis advanced to explain apical dominance.

Despite general acceptance of the nutrient hypothesis, there were contemporaneous suggestions that apical dominance may be caused by "internal plant secretions" (Went and Thimann 1937, Martin 1987). The existence of such substances in plants had previously been suggested in research conducted between 1870 and 1880 addressing root gravitropism and shoot phototropism (Heslop-Harrison 1980). The potential production of a chemical signal in the apical meristem presented an alternative interpretation for the physiological mechanism of apical dominance. Bud growth could potentially be inhibited by the production of a translocatable growth-inhibiting substance in the apical meristem, rather than simply by the ability of the apical meristem to function as the predominant nutrient sink within plants. Indirect evidence for this "inhibitor" hypothesis was later produced from girdling experi-

ments, but the chemical identity of the putative growth-inhibiting substance remained unknown (Reed and Halma 1919, Harvey 1920, Snow 1925).

The discovery of the plant hormone auxin (IAA) during the late 1920's undoubtedly provided an exciting candidate for the growth-inhibiting substance. Thimann and Skoog (1934), in a now classic study, demonstrated the involvement of IAA in apical dominance of bean (*Vicia faba* L.) seedlings. Agar blocks containing IAA placed atop a decapitated (removal of the apical meristem only) stem maintained bud inhibition while similar placement of agar blocks without IAA enabled bud growth to occur. This investigation also demonstrated that IAA was produced in large quantities in the apical meristem and young, developing leaves while inhibited lateral buds and older plant organs contained only minimal quantities. This particular finding verified prior claims that the developing leaves and apical meristem were the organs responsible for bud inhibition (Snow 1929). On the basis of this evidence, IAA produced in the apical meristem was proposed to directly inhibit axillary bud growth establishing the "direct hypothesis of auxin action" (Thimann and Skoog 1934, Phillips 1969).

The direct hypothesis of auxin action (direct hypothesis) was not accepted unconditionally. Questions arose because elements of this hypothesis contradicted the widely accepted function of IAA in plants. IAA was regarded exclusively as a growth-promoting plant hormone at that time, but the direct hypothesis proposed that IAA produced in the apical meristem was translocated down the stem to the axillary buds where it suppressed bud growth (Thimann and Skoog 1933, 1934). Therefore, IAA must have had the enigmatic ability to both stimulate and inhibit growth depending on whether it originated in the apical meristem or axillary buds. Thimann (1937) suggested that this contradiction could be explained if bud inhibition resulted from supraoptimal IAA concentrations in the stem. It was known at the time that upon release from inhibition, axillary buds produced only one-half the IAA concentrations of the apical meristem (Thimann and Skoog 1933, 1934). This provided the basis for a revised version of the direct hypothesis indicating that the growth of each individual plant organ was promoted by distinct IAA concentrations (Thimann 1937). The highest IAA concentrations promoted stem growth, intermediate concentrations promoted bud growth, and the lowest concentrations pro-

moted root growth.

Following revision, the direct hypothesis encountered additional limitations. First, the amount of IAA in the agar blocks used to replace the apical meristem and maintain bud inhibition was 11 times greater than that recovered from apical meristems by diffusion into agar blocks (Thimann and Skoog 1934). Second, subsequent attempts to inhibit bud growth by replacing the apical meristem with an IAA source did not always maintain axillary bud inhibition (e.g., Jacobs and Bullwinkle 1953). Third, axillary buds furthest from the apical meristem were less likely to break inhibition and grow than buds located closer to the apical meristem in some species (Went and Thimann 1937, Went 1939). This pattern of bud inhibition was believed at the time to be inconsistent with responses predicted by the direct hypothesis (Went 1939). Fourth, there was no satisfactory explanation of the mechanism by which supraoptimal IAA concentrations in the stem blocked bud growth.

Limitations of the direct hypothesis led to 3 alternative proposals for the physiological mechanism of apical dominance. All were based on the premise that the role of IAA in apical dominance was indirect. The first of these was the "diversion" hypothesis (Went 1938, 1939). This hypothesis proposed that IAA transport down the stem caused root-produced substances required for bud growth to move toward the apical meristem bypassing the axillary buds. Bud inhibition was overcome when a sufficient amount of growth substances accumulated in the stem to "spill over" into the inhibited axillary buds. These root-produced substances were assumed to be hormonal, rather than nutritional, in nature. The mechanism by which IAA induced transport of the root-produced substances in the opposite direction and the identity of these compounds were unknown.

The second alternative hypothesis was based on evidence suggesting that IAA must be directly introduced into the vascular system at a point above the bud to inhibit growth (Van Overbeek 1938). Once in the vascular tissue, it was proposed that IAA adhered to cell walls and impeded vascular transport. This "blocking" hypothesis specifically stated that IAA adhered to the inner cell walls of the vascular traces connecting the bud with the parental shoot blocking the entry of nutrients, water, and other factors required for bud growth (Van Overbeek 1938).

Minor variations of the blocking hypothesis were proposed following the introduction of the original hypothesis (Sorokin and Thimann 1964, Panigrahi and Audus 1966). Collectively, these hypotheses, including the original blocking hypothesis, have been termed the "vascular connections" hypothesis (Phillips 1969, 1975). The vascular connections hypothesis was eventually abandoned during the 1970's for 2 main reasons. First, bud growth following decapitation is detectable many hours before vascular connections become evident between the parental shoot and axillary buds (Cutter 1975). Second, axillary buds with well-developed vascular traces can remain inhibited while those with incomplete vascular traces can be released from inhibition following decapitation (McIntyre 1977).

The third alternative suggesting an indirect role for IAA in the mechanism of apical dominance was a modified version of the inhibitor hypothesis. Snow (1940) suggested that IAA stimulated the production of a chemical inhibitor which was capable of moving into the axillary buds to inhibit growth. No such inhibitor was isolated and, consequently, the revised inhibitor hypothesis gained only limited acceptance.

Grasses

Research information addressing the regulation of tiller initiation in perennial grasses was very limited prior to 1940. Essentially all investigations of the physiological mechanisms of apical domi-

nance during the first half of the century were conducted with dicots. The extent to which the findings from this work could be extended to the regulation of tillering in grasses was unknown. The most commonly held perspective prior to 1940 was that tiller initiation was primarily correlated with nutrient availability, phenological development, and the occurrence of favorable conditions for growth rather than regulated by a hormonal mechanism (Olmstead 1941, Gardner 1942). This perception was very likely promoted by the production-oriented agronomic research conducted with cereals early in the century (Bunting and Drennan 1966).

Leopold (1949) conducted the first work investigating the possibility of a hormonal basis for the regulation of tiller initiation in grasses. Apical meristems of the annuals barley (*Hordeum vulgare* L.) and teosinte (*Euchlaena mexicana* Schrad.) were destroyed *in situ* with a needle in 20 plants of each species. A synthetic auxin (α -naphthalene acetic acid) was injected in the position of the destroyed apex in one-half of the plants with a hypodermic needle at weekly intervals for 3 weeks. The limited data from this experiment were interpreted to indicate that IAA diffusing from the tiller apical meristem directly inhibited the growth of axillary buds (Table 2). Although Leopold (1949) based his interpretation entirely on the direct hypothesis developed with dicots 16 years

Table 2. Data from Leopold (1949) addressing the role of the apical meristem in the regulation of tillering in barley (*Hordeum vulgare* L.) and teosinte (*Euchlaena mexicana* Schrad.). These data provided the basis for accepting the direct hypothesis of auxin action as the physiological mechanism responsible for apical dominance in grasses.

Treatment	Barley		Teosinte	
	Tillering	Not tillering	Tillering	Not tillering
	----- (Number of plants) -----			
Untreated control	0	10	3	7
Apex destroyed	8	2	9	1
Apex destroyed, IAA added	0	10	3	7

earlier, the data do not clearly exclude the possibility of an indirect role for IAA or that the amount of injected IAA was simply toxic (Bunting and Drennan 1966, Williams and Langer 1975). Nevertheless, the limited data derived from these 2 annual grasses apparently established the current perception that tiller initiation in perennial grasses is regulated by a hormonal mechanism.

In summary, 5 major hypotheses had been advanced by 1940 to explain the physiological mechanism of apical dominance in dicots (Table 1). No single hypothesis was accepted unanimously, but none had been convincingly refuted either. The physiological mechanisms of apical dominance were largely unexplored in grasses until Leopold (1949) suggested that tillering was directly regulated by IAA produced in the apical meristem.

Adoption of the Apical Dominance Concept by Range Science

The apical dominance concept has long been invoked by the range science profession to explain the regulation of tillering in grasses and especially tiller initiation in response to defoliation. Apical meristem removal is assumed to stimulate axillary bud growth and promote tiller initiation. The stimulation of bud growth presumably occurs because the direct inhibitory influence exerted by the apical meristem is removed. This interpretation of the regulation of tiller initiation in perennial range grasses has been exclusively presented in all major range science texts (Stoddart and

Smith 1943, Sampson 1952, Stoddart and Smith 1955, Heady 1975, Stoddart et al. 1975, Holechek et al. 1989).

The apical dominance concept was introduced into the range science profession quite early and predated the experimental work on grasses by Leopold (1949). Anecdotal statements asserting apical meristem control over axillary bud growth in grasses appeared in the first major range management text (Stoddart and Smith 1943, p. 132, 142). Neither citations nor experimental evidence were provided, making it difficult to verify the origin or assess the validity of this concept to grasses. The concept of apical dominance appears to have been initially incorporated into the profession

based on empirical observation rather than on experimental evidence developed with dicots during the previous decade.

The initial physiological interpretation of apical dominance in grasses in the range science literature emphasized a hormonal mechanism. Branson (1956) was the first to formally introduce the direct hypothesis to the range literature based on the research of Leopold (1949). Rechenhain (1956) also briefly described the physiological process of axillary bud growth following defoliation or apical meristem removal in terms of the direct hypothesis. However, neither citations nor experimental evidence were provided by Rechenhain (1956). Jameson (1963) concluded from a review of the

Table 3. Summary of selected literature demonstrating the inconsistent response of tiller initiation in various perennial grasses following grazing, clipping, or decapitation.

Species	Reference	Treatment
	Tillering stimulated	
Little bluestem <i>Schizachyrium scoparium</i> (Michx.) Nash	Jameson and Huss (1959)	Elongated culms clipped to 6 or 12.5 cm
Italian ryegrass <i>Lolium multiflorum</i> (Lam.)	Laidlaw and Berrie (1974)	Removal of the two youngest expanding leaves and decapitation
Arizona cottontop <i>Trichachne californica</i> (Benth.) Chase	Cable (1982)	Decapitation at several phenological stages
Little bluestem <i>Schizachyrium scoparium</i> var. <i>frequens</i> Hubb.	Butler and Briske (1988)	Plants grazed by cattle leaving the apical meristem intact. Stimulation was short-lived because total tiller numbers did not differ from ungrazed plants at the end of the growing season.
Red oatgrass <i>Themeda triandra</i> Forsk.	Richards et al. (1988)	Decapitation or defoliation
Guineagrass <i>Panicum maximum</i> Jacq. var. <i>trichoglume</i> Eyles		
Tanglehead <i>Heteropogon contortus</i> (L.) P. Beauv. ex Roem. Schult.		
Crested wheatgrass <i>Agropyron desertorum</i> (Fisch. ex Link) Schult.	Richards et al. (1988)	Defoliation
Bluebunch wheatgrass <i>Pseudoroegneria spicata</i> (Pursh) A. Löve		
	Tillering not stimulated	
Blue grama <i>Bouteloua gracilis</i> (H.B.K.) Lag. ex Steud.	Branson (1956)	Defoliation to various heights and frequencies
Western wheatgrass <i>Pascopyrum smithii</i> (Rydb.) A. Löve		
Kentucky bluegrass <i>Poa pratensis</i> (L.)		
Bluebunch wheatgrass <i>Pseudoroegneria spicata</i> (Pursh) A. Löve		
Needleandthread <i>Stipa comata</i> Trin. and Rupr.		
Big bluestem <i>Andropogon gerardii</i> Vitman	Vogel and Bjugstad (1968)	Defoliation without decapitation
Little bluestem <i>Schizachyrium scoparium</i> (Michx.) Nash		
Indiangrass <i>Sorghastrum nutans</i> (L.) Nash		
Pinegrass <i>Calamagrostis rubescens</i> Buckl.	Stout et al. (1981)	Biweekly defoliations to 3 heights over 4 growing seasons
Fine thatching grass <i>Hyparrhenia filipendula</i> Stapf.	Coughenour et al. (1985a, 1985b)	Defoliation with high nitrogen levels
Red oatgrass <i>Themeda triandra</i> Forsk.		
Crested wheatgrass <i>Agropyron desertorum</i> (Fisch. ex Link) Schult.	Richards et al. (1988)	Decapitation
Bluebunch wheatgrass <i>Pseudoroegneria spicata</i> (Pursh) A. Löve		
Crested wheatgrass <i>Agropyron desertorum</i> (Fisch. ex Link) Schult.	Olson and Richards (1988a)	Moderate and heavy grazing by cattle

early literature that IAA produced in the apical meristem directly inhibited axillary bud growth, based on the evidence presented by Thimann and Skoog (1933, 1934) and Leopold (1949). He also inferred that the apical meristem or rapidly elongating leaves must be removed to stimulate tiller initiation in grasses. Jameson (1963) appears to have provided the last critical assessment of the physiological mechanisms of apical dominance in grasses in the range science literature.

Interpretive Value of the Apical Dominance Concept

The essential feature of the apical dominance concept to the range science profession is its interpretive value concerning the timing and magnitude of tiller initiation in grasses. Apical meristem removal should release axillary buds from inhibition irrespective of the specific physiological mechanisms responsible for apical dominance. The apical meristem is assumed to be the source of the principal signal inducing bud inhibition in all of the mechanisms which have been proposed. Consequently, apical meristem removal should consistently stimulate tillering by eliminating the source of inhibition.

However, a large amount of evidence demonstrates that tiller initiation is not consistently stimulated following clipping or grazing. In extensive reviews of the early literature, both Ellison (1960) and Jameson (1963) concluded that grazing generally suppressed tillering in perennial grasses. Jameson (1963) suggested that minimal tiller initiation in response to defoliation probably resulted from failure to remove the apical meristem. In a test of the applicability of the direct hypothesis to 5 perennial grasses, Branson (1956) found no evidence that tillering was stimulated in response to clipping to various heights and frequencies (Table 3). Data from more recent investigations also demonstrate inconsistent tillering

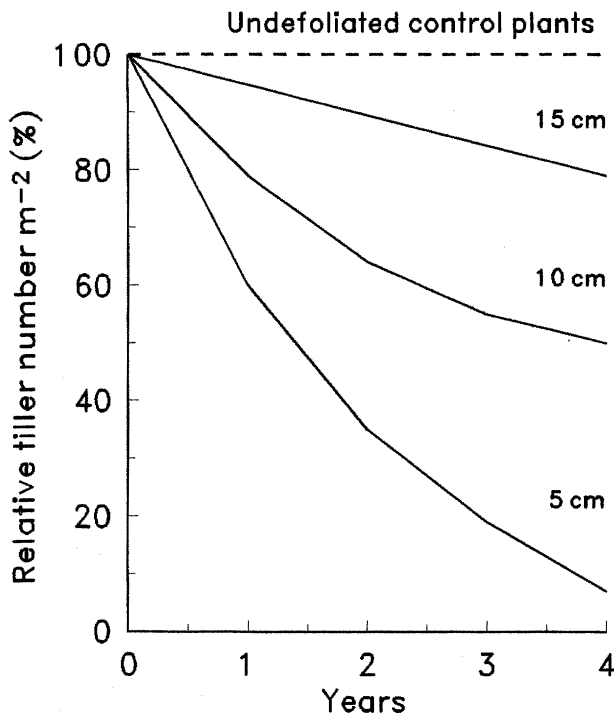


Fig. 2. Number of pinegrass (*Calamagrostis rubescens* Buckl.) tillers m⁻², expressed as a relative percentage of the number of tillers m⁻² in undefoliated populations, in response to biweekly clipping to 5, 10, and 15 cm stubble heights over 4 successive years. Data demonstrate that tillering in this species population was not stimulated by defoliation over the long-term. Redrawn from Stout et al. (1981).

responses following defoliation of individual plants (Table 3) and species population (Fig. 2).

Inconsistent tillering responses to defoliation may partially be explained on the basis of whether or not the apical meristem was actually removed by defoliation or grazing (Jameson 1963). Phenological stage of plant development at the time of defoliation is an important factor in this regard because internode elongation increases the probability of apical meristem removal (Branson 1953, Jewiss 1972, Westoby 1980). However, available data concerning tiller initiation in response to defoliation at various stages of plant development are also inconsistent and difficult to interpret (e.g., Jameson and Huss 1959; Langer 1959; Vogel and Bjugstad 1968; Cable 1982; Olson and Richards 1988a, 1988b). Selective removal of the apical meristem, while the leaves remain intact, does not consistently stimulate tiller initiation in all grass species (Laidlaw and Berrie 1974, Richards et al. 1988, Fig. 3). Conversely, tillering can occur in response to defoliation or grazing even if apical meristems have not been removed (Butler and Briske 1988).

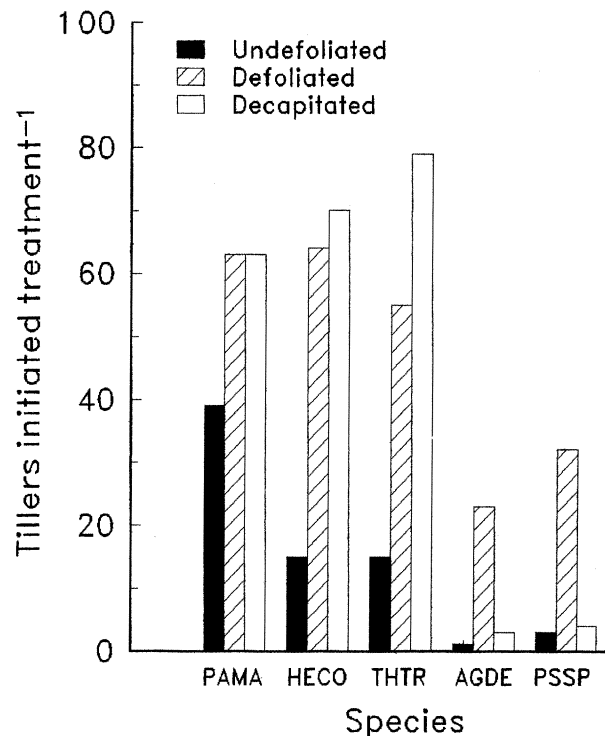


Fig. 3. Total number of tillers initiated treatment⁻¹ 4-5 weeks following defoliation to 7-10 cm stubble height (removal of leaves and apical meristems) or decapitation (removal of apical meristems only) in comparison with undefoliated plants for 5 perennial grass species. Species are PAMA, *Panicum maximum* Jacq. var. *trichoglume* Eyles; HECO, *Heteropogon contortus* (L.) P. Beauv. ex Roem. and Schult.; THTR, *Themeda triandra* Forsk.; AGDE, *Agropyron desertorum* (Fisch. ex Link) Schult. and PSSP, *Pseudoroegneria spicata* (Pursh) A. Löve. Redrawn from Richards et al. (1988).

Traditional emphasis on the direct hypothesis as the sole physiological mechanism of apical dominance in grasses may be partially responsible for the widely held perception that defoliation consistently stimulates tillering despite considerable evidence to the contrary.

Another potential source of confusion concerning tiller initiation in response to defoliation is the time interval during which tillering is monitored. Tillers are frequently initiated within 2 to 3 weeks of defoliation and are much more obvious following partial canopy removal (Olson and Richards 1988b). However, this short-term "flush" of tiller initiation following defoliation may be mis-

leading if not evaluated for one or more growing seasons. For example, tiller recruitment of crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult.) following spring grazing did not increase tiller replacement the following growing season because of greater overwinter tiller mortality in grazed plants than in ungrazed plants (Olson and Richards 1988a). Similarly, tillering increased immediately following grazing of little bluestem (*Schizachyrium scoparium* var. *frequens* Hubb.), but the total number of tillers was not significantly greater in grazed than in ungrazed plants at the end of the growing season (Butler and Briske 1988). Although grazing extended the season of tiller initiation in grazed plants, these plants produced significantly fewer tillers during periods of maximal tiller recruitment in ungrazed plants. Therefore, defoliation may simply alter the timing of tiller initiation rather than increase the total number of tillers initiated over the long-term. These data collectively demonstrate that the interpretive value of the apical dominance concept is insufficient to explain tiller initiation in perennial grasses.

Environmental Influences on Tiller Initiation

Radiation quantity, photoperiod, water availability, mineral nutrition, and temperature, acting singly or in combination, have long been recognized to influence tillering (Table 4). In general,

Table 4. Generalized effects of major abiotic variables on tiller initiation in perennial grasses. Radiation quality effects are from Deregibus et al. (1985) and Casal et al. (1987) and the effects of all other variables are summarized from Langer (1963).

Abiotic variable	Response of tillering
Radiation quantity	Increases with increasing photosynthetic photon flux density.
Radiation quality	Increases with increases in the red/far-red ratio.
Photoperiod	Decreases as natural photoperiod increases.
Temperature	Increases as temperature approaches an optimum for growth, but further increases reducing tillering. Interactions with other environmental variables are important.
Water	Increases with increasing soil water availability.
Soil nitrogen	Increases with increasing nitrogen availability.

tiller initiation increases as environmental variables become more conducive to overall plant growth. Considering the temporal and spacial variability of climate and resource distribution on rangelands, the regulatory influence of environmental variables on tiller initiation are undoubtedly substantial.

Radiation quality has been demonstrated to influence tiller initiation in several grasses. Tillering is reduced by a decrease in the ratio of red/far-red radiation independent of the availability or interception of photosynthetically active radiation (Deregibus et al. 1985; Casal et al. 1987, 1990). Reductions in the red/far-red ratio (ratio of spectral photon flux in 10-nm bands centered on 660 nm for red and 730 nm for far-red radiation) commonly arise under natural conditions as wavelengths under 700 nm are selectively attenuated as radiation passes through plant canopies (Smith 1982). Alternatively, the red/far-red ratio may be reduced by far-red radiation reflected from leaves of neighboring plants (Ballaré et al. 1987, 1990). Changes in the red/far-red ratio are detected by the pigment phytochrome, which provides a sensitive photosensory mechanism for monitoring the red/far-red ratio within the immediate vicinity of the plant. The physiological processes associated with phytochrome-mediated reductions in tiller initiation and apical dominance are not clearly understood.

Defoliation may promote tillering without disturbing the apical

meristem by partially removing the plant canopy and increasing the red/far-red ratio (Deregibus et al. 1985, Deregibus and Trlica 1990). In this context, the red/far-red ratio may function as an environmental signal indicating increased resource availability within the immediate vicinity of the plant. However, canopy removal by defoliation simultaneously alters radiation quantity, temperature, plant water relations, and other microenvironmental and physiological variables important to plant growth. Any of these variables, either singly or in combination, may be as important as radiation quality in affecting tiller initiation following defoliation. Although radiation quality has been demonstrated to influence tiller initiation in several grasses, considerable research is required before definitive ecological and managerial conclusions can be established concerning its relative importance.

Intra- and interspecific plant competition also influences tiller initiation by affecting resource availability. Tiller initiation in individual bunchgrasses increases following the removal of conspecific neighbors (Briske and Butler 1989, Olson and Richards 1989) and nitrogen fertilization (Olson and Richards 1989). Competitive interactions also exert a substantial influence on tiller initiation in defoliated plants (Mueggler 1972). Defoliated big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.) plants initiate fewer tillers when grown at medium and high plant densities than defoliated plants grown at low plant densities (Fig.

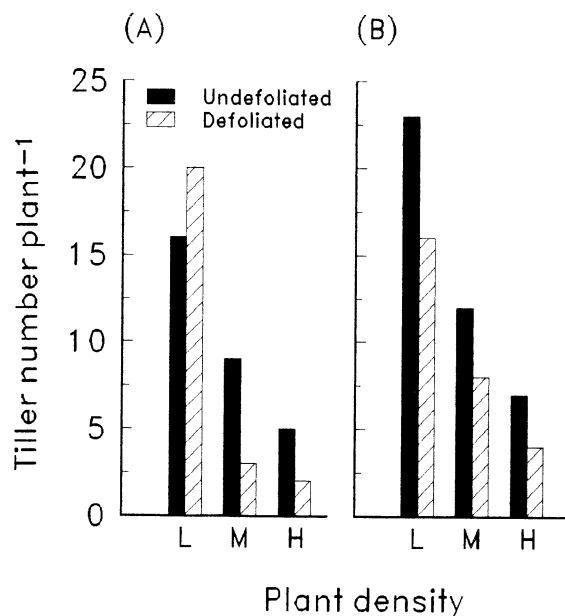


Fig. 4. Tiller number plant⁻¹ recorded at the end of the growing season for (A) big bluestem (*Andropogon gerardii* Vitman) and (B) switchgrass (*Panicum virgatum* L.) grown at 3 plant densities and subjected to a single early season defoliation to a 4-cm stubble height. L = low density (56 plants m⁻²), M = medium density (226 plants m⁻²) and H = high density (452 plants m⁻²). Redrawn from Hartnett (1989).

4). Despite demonstrations of the substantial influence of competition on tiller initiation in perennial grasses, it has traditionally received far less attention than other environmental variables.

Current Perspectives on the Mechanisms of Apical Dominance

The physiological mechanism of apical dominance is currently thought to have either a hormonal or nutritional basis. However, hormonal interpretations have traditionally received greater emphasis and attention. This indicates greater acceptance of the hormonal interpretation for the mechanism of apical dominance, but also

reflects the discovery of new classes of plant hormones since 1960 and recent technological advances in hormone quantitation. However, these methodological advances have not contributed to a clearer understanding of the mechanism of apical dominance (Cline 1991). This section briefly describes the current perspectives concerning the hormonal and nutritional mechanisms of apical dominance.

Hormonal Mechanism

Before the 1950's, IAA was the only growth-promoting plant hormone known to western science and was believed to regulate all plant growth processes. The discovery of a second category of growth-promoting plant hormones in the late 1950's introduced the possibility for alternative explanations for plant growth regulation. Wickson and Thimann (1958) were the first to demonstrate that a synthetic cytokinin, the generic name for compounds that promote cell division in plants in the presence of IAA, applied directly to inhibited axillary buds could transiently reverse IAA-induced growth inhibition. This finding was interpreted to indicate that cytokinins, in addition to IAA, have a fundamental role in the apical dominance mechanism.

More recent studies confirm the conclusion of Wickson and Thimann (1958) suggesting that bud inhibition is induced by a cytokinin deficiency. The direct application of cytokinin to inhibited buds promotes bud growth in dicots (Panigrahi and Audus 1966, Sachs and Thimann 1967, Schaeffer and Sharpe 1969, Ali and Fletcher 1970, but see Tucker and Mansfield 1973, Nagao and Rubinstein 1975) and grasses (Langer et al. 1973, Johnston and Jeffcoat 1977, Harrison and Kaufman 1980, Isbell and Morgan 1982). Cytokinin concentrations have also been shown to increase in sorghum (*Sorghum bicolor* M.) crown sections with attached axillary buds 1 day after defoliation (Nojima et al. 1985). Axillary bud growth began within 2 days of defoliation, suggesting a causal relationship between bud growth and elevated cytokinin levels.

Demonstrations that cytokinins can release axillary buds from inhibition have provided the foundation for a sixth hypothesis of apical dominance (Table 1). The "cytokinin deficiency" hypothesis, as termed here, indicates that IAA transported down the stem from the apical meristem blocks cytokinin synthesis or utilization in axillary buds thereby inhibiting growth (Phillips 1975). The cytokinin deficiency hypothesis has incorporated and replaced the direct hypothesis as the most current hormonally based interpretation for the mechanism of apical dominance (Cline 1991).

Despite wide acceptance, many aspects of the cytokinin deficiency hypothesis remain unresolved. For example, it is not known how IAA blocks cytokinin synthesis or utilization in axillary buds. One suggestion is that IAA stimulates that catabolism of cytokinin during transport to axillary buds from the site of cytokinin synthesis in roots (Harrison and Kaufman 1984). However, disagreement exists as to whether cytokinins are synthesized exclusively in roots (cf. Lee et al. 1974, Skene 1975, Wang and Wareing 1979, Kuiper and Kuiper 1988). For example, apical meristem removal stimulated growth of inhibited buds on rootless plants, suggesting the occurrence of an alternative source of cytokinins to those produced in the roots (Wang and Wareing 1979). If cytokinin synthesis is limited to roots as is generally believed, then some bidirectional transport mechanism involving IAA and cytokinins must operate to prevent root-produced cytokinins from entering the buds to initiate growth (Woolley and Wareing 1972).

Plant hormones other than IAA and cytokinin have been postulated to function in apical dominance (Table 5). Direct application of the growth-inhibiting hormone abscisic acid (ABA) to growing axillary buds on decapitated plants inhibits bud growth (Arney and Mitchell 1969, Harrison and Kaufman 1980). Conversely, ABA concentrations in inhibited buds decline significantly within hours after apical meristem removal in several plant species

Table 5. Putative roles of plant hormones in apical dominance summarized from Tamas (1987). Date indicates the year during which each hormone was first isolated from a vascular plant source.

Plant hormone	Date	Role in apical dominance
Indole-3-acetic acid	1944	Principal chemical signal inhibiting axillary bud growth by blocking cytokinin synthesis or utilization in the axillary bud.
Cytokinins	1963	Release axillary buds from inhibition.
Abscisic acid	1963	Inhibits axillary bud growth, but information is limited.
Gibberellins	1960	Associated with bud elongation following release from inhibition, but direct involvement in apical dominance is questionable.
Ethylene	1934	Inhibits axillary bud growth in the presence of IAA, but evidence is limited and contradictory.

(Tucker and Mansfield 1973, Nojima et al. 1989, Gocal et al. 1991). The release of ethylene, a gaseous hormone often associated with senescence and fruit-ripening processes, has been reported to peak at the time of bud swelling in oat (*Avena sativa* L.) stem segments (Harrison and Kaufman 1982). Foliar-applied synthetic ethylene compounds also appear to stimulate bud elongation in barley (Woodward and Marshall 1988). Although the significance of these correlative data concerning ABA and ethylene remains to be demonstrated, the potential involvement of hormones other than IAA and cytokinin suggest that the cytokinin deficiency hypothesis may also be an incomplete assessment of the actual apical dominance mechanism (Phillips 1975, Hillman 1984, Tamas 1987).

Nutritional Mechanism

Despite the large amount of emphasis on hormonal regulation of bud growth, a renewed interest in nutritional interpretations for the mechanism of apical dominance has occurred over the last 30 years. Gregory and Veale (1957) were among the first to resurrect the nutritive hypothesis following its decline during the early 1900's. Their data suggested that the degree of apical dominance exhibited by common flax (*Linum usitatissimum* L.) was dependent on the nitrogen and carbohydrate status of the plant. They concluded that competition occurred among axillary buds and the apical meristem for these limiting resources within the plant.

Numerous investigations since Gregory and Veale (1957) have implicated resource limitations as the cause of axillary bud inhibition (McIntyre 1972, Fletcher and Dale 1974, Prasad et al. 1989, McIntyre and Cessna 1991). For example, Aspinall (1961) demonstrated that tiller initiation in barley was reduced by low nitrogen levels, but that tillering could be stimulated at any time by nitrogen addition. Nitrogen availability can also influence tiller initiation in response to decapitation. Decapitated ryegrass plants grown with high nitrogen availability produced significantly more secondary tillers than decapitated plants with low nitrogen availability. The total number of primary tillers did not differ between plants with decapitated or intact apical meristems, but decapitated plants initiated tillers earlier than plants with intact meristems (Laidlaw and Berrie 1974). Other researchers have demonstrated that in addition to nutrient limitations, water (Cottignies and Jennane 1988, McIntyre and Damson 1988) and carbohydrate supply (Mitchell 1953; McIntyre 1967, 1970; Fletcher and Dale 1974) exert important influences on axillary bud growth.

The nutritional interpretation for the mechanism of apical dominance is based on the correlative relationship between bud growth

and nutrient availability. For example, bud growth has been observed to increase within 6 hours following the addition of nitrogen (McIntyre and Cessna 1991). However, as Phillips (1975) has pointed out, it is impossible to conclude from such evidence that apical dominance is purely a nutritionally regulated response. Bud growth in response to increased nutrient availability may simply be 1 component of an overall increase in plant growth as opposed to a specific growth stimulation of inhibited buds. Similarly, higher nutrient concentrations have been found in buds released from inhibition in comparison with their inhibited counterparts (McIntyre 1972, 1977), but these correlative data do not necessarily imply a causal relationship. Greater nutrient concentrations in growing buds may more accurately reflect the result, rather than the cause, of axillary bud growth (Jewiss 1972, Rubinstein and Nagao 1976). Additionally, it is not known whether bud growth following apical meristem removal, exogenous cytokinin application, or nitrogen addition promote bud growth by similar physiological processes (Rubinstein and Nagao 1976). Consequently, it is difficult to deny the partial involvement of resource availability in apical dominance; but it has yet to be established that axillary bud growth is purely a nutritionally regulated response.

Nutritional and hormonal interpretations for the mechanism of apical dominance have traditionally been viewed as mutually exclusive alternatives. Experimental information necessary to distinguish between these 2 interpretations must establish whether the apical meristem functions primarily as the predominant sink for available resources within the plant or site of synthesis for IAA which may directly or indirectly inhibit bud growth. The absence of this information in the literature is not surprising considering the technical difficulties involved. However, it may be inappropriate to assume *a priori* that hormonal and nutritional regulation of apical dominance are mutually exclusive. Hormones play critical roles in plant growth and development which may indirectly affect nutrient requirements and distribution and, in turn, nutrient availability may affect hormone biosynthesis and metabolism (e.g., Salama and Wareing 1979, Thorsteinsson and Eliasson 1990). Therefore, it seems plausible that nutritional and hormonal mechanisms may interact to influence bud growth in apical dominance, but only limited evidence exists to support this suggestion (Phillips 1975).

Conclusions

The physiological mechanisms responsible for apical dominance have been investigated in plant physiology and various applied fields for nearly a century. Although 6 major hypotheses have been proposed, none is totally satisfactory and a definitive understanding of the mechanism of apical dominance remains elusive. The cytokinin deficiency hypothesis is currently the most widely accepted interpretation for the physiological mechanism of apical dominance. This hypothesis suggests that bud inhibition results from IAA blockage of cytokinin synthesis or utilization in axillary buds. However, numerous aspects of this hypothesis remain unresolved, suggesting that it may also be an incomplete interpretation.

The apical dominance concept was introduced into the range science literature in the first range management text published in 1943 as anecdotal statements asserting apical meristem control over axillary bud growth in grasses. The experimental information addressing the physiological mechanisms of apical dominance in dicots published prior to 1940 did not appear to have directly influenced concept adoption by the profession. Consequently, it is difficult to verify the origin or assess the validity of the concept as it was initially applied to grasses because neither citations nor experimental evidence were provided.

The first physiological interpretation of apical dominance in grasses appeared in the range science literature (Branson 1956)

13 years after the apical dominance concept was introduced to the profession by Stoddart and Smith (1943). The range science profession appears to have adopted the direct hypothesis of auxin action proposed during the 1930's and still relies exclusively on this hypothesis to interpret tiller initiation in grasses. However, the direct hypothesis was abandoned by plant physiologists during the late 1950's based on experimental and interpretive inconsistencies and the demonstration of cytokinin-induced axillary bud growth. Although the direct hypothesis is outdated, the apical meristem and IAA still assume pivotal roles in the cytokinin deficiency hypothesis because IAA produced in the apical meristem is assumed to prevent cytokinin synthesis or utilization in axillary buds, thereby inhibiting their growth.

Regardless of the particular mechanistic interpretation invoked to explain apical dominance, the validity of the concept must be based on consistent stimulation of tiller initiation following apical meristem removal. However, apical meristem removal does not consistently explain tiller initiation in perennial grasses as is commonly assumed. Numerous examples have been documented where tillering was not promoted by apical meristem removal and others have substantiated the occurrence of tillering following defoliation even though apical meristems were not removed. These inconsistencies demonstrate that the apical dominance concept is an overly restrictive interpretation for the regulation of tiller initiation in perennial grasses.

Several environmental variables are known to influence tiller initiation either singly or in combination. Tillering generally increases as abiotic variables collectively become more conducive to plant growth. Biotic variables, including grazing and competition, also exert a substantial influence on the timing and magnitude of tiller initiation. In spite of the evidence documenting the regulatory role of abiotic and biotic variables, these variables have received far less emphasis than hormonal explanations of tillering. The extreme spatial and temporal variability of environmental variables and resource distribution on rangelands increases the importance of these factors in the regulation of tillering by potentially overriding or constraining the physiological mechanisms of apical dominance (Harper 1964, Archer and Smeins 1991, Briske 1991). Consequently, environmental variables may play an equal or greater role than the physiological mechanisms responsible for apical dominance in establishing the timing and magnitude of tiller initiation in grasses.

Molecular and biochemical plant research will undoubtedly provide a more definitive interpretation of the mechanism of apical dominance. Major advancements will likely occur in hormone physiology and the genetic regulation of plant growth and development. However, advances in the molecular and biochemical mechanisms of apical dominance may not directly translate to a greater understanding of apical dominance within the whole plant. In addition, the consequences of apical dominance in species populations and grassland communities are influenced by a variety of abiotic and biotic variables which are beyond the scope of plant molecular biology and biochemistry. Consequently, researchers in the applied sciences must continue to reevaluate and revise models of apical dominance appropriate to the objectives of their specific professions.

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