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SYMPOSIUM ON THE PHYLLOCHRON

Importance of the Phyllochron in Studying Development and Growth in Grasses

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ABSTRACT

The phyllochron, which is defined as the interval between similar growth stages of successive leaves on the same culm, has been used extensively to describe and understand development of grasses. The purpose of this paper is to introduce seven papers presented as part of the symposium *Understanding Development and Growth in Grasses: Role of the Phyllochron Concept*. Environmental (temperature, water, and day length) factors and genetics affect the duration of the phyllochron. The following seven papers broaden the discussion of these topics and present new concepts about how the environment and genetics impact the relationship between leaf appearance and whole plant development.

THIS PAPER and the seven that follow summarize presentations from the symposium *Understanding Development and Growth in Grasses: Role of the Phyllochron Concept* delivered at the Crop Science Society of America meetings in Cincinnati, OH, on 10 Nov. 1993. The objective of the symposium was to present current information on the use of the phyllochron (simply defined as the time interval between appearance of successive leaves on a culm) concept to understand and describe development in grasses and to provide a forum for interchange of ideas on using the phyllochron in the study of development. The objective of this paper is to introduce the papers, establish definitions of terms used, and briefly discuss environmental factors affecting rate of leaf appearance.

The grass family is one of the most important families in the plant kingdom. Members of this family are used extensively for food, feed, fiber, and shelter. The small-grain cereals, corn (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench], and most forages, are members of this family. The three most widely grown crop species, wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and corn are grasses (USDA, 1992). Without forage grasses, the livestock industry, as we know it, would not exist.

From an agricultural perspective, the caryopsis is the critical part of grain crops. Most of our knowledge centers on events and processes related to development and growth of the kernel. Most numerical scales to describe growth of grasses emphasize stages during kernel development (Hanway, 1963; Large, 1954; Vanderlip, 1979; Waldren and Flowerday, 1979; Zadoks et al., 1974). The most widely used exception is the Haun scale (Haun, 1973), which is more useful for defining vegetative than reproductive development. Recently, the importance of vegetative development and growth has been recognized by others and greater detail has been added to existing developmental scales during the vegetative phase (Ritchie et al., 1986; Zadoks et al., 1974). The importance of vegetative development has always been recognized in forage grasses because vegetative material is economically important to livestock production (Moore et al., 1991; Simon and Park, 1983; West, 1990).

Development and growth are distinct, but related, processes. Unfortunately, these processes are often confused or conceived as being synonymous. In some cases, this confusion does not limit understanding of the processes; however, at other times, the distinction between the two processes is critical to understanding concepts.

As discussed by Salisbury and Ross (1969), Sinnott (1960), and Wetmore and Steeves (1971), growth can be defined several ways, but the most acceptable is a permanent increase in volume. Because volume is defined by the product of three linear dimensions, growth can also be defined simply as the irreversible increase in physical dimension of an individual or organ with time. Therefore, examples of growth are irreversible lengthening of leaf blade tissue or increase in leaf area. In agriculture, where the purpose of most enterprises is to convert solar energy into dry matter, an equally useful definition of growth is increase in dry weight.

Development is somewhat more difficult to define (Greulach, 1973; Salisbury and Ross, 1969). It includes the processes of organ initiation (morphogenesis) but

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Abbreviation: GDD, growing degree days.

extends to differentiation and ultimately must include the process of senescence. The process by which plants, organs, or cells pass through various identifiable stages during their life cycle can be considered a functional definition of development.

Generally, growth and development occur simultaneously. However, development and growth are not mutually inclusive nor exclusive. Under specific conditions, one may occur without the other. Environmental stress frequently allows development to advance while stopping growth. An example of simultaneous development and growth is the advance in Haun stage. Because most Haun development stages are defined by the ratio of leaf lengths, if leaves do not grow, lengths do not change, and no development is measured.

In discussing development, an implicit dimension is time. In this paper and throughout this symposium, the concept of time is not limited to a temporal definition (i.e., passing of minutes, hours, or days). Instead, a broader concept is used where the interval between events can be measured in many ways: clock time, heat units, or photothermal units. The only restriction is that the measure of time meaningfully reflects the response of the plant to the passage of these intervals.

Several terms have been used interchangeably to describe the rate of leaf appearance: plastochron, auxochron, and phyllochron. The oldest of these terms, plastochron (or plastochrone in some British literature), was originally defined by Askenasy (1880), as cited by Erickson and Michelini (1957), as the interval between formation of two successive internode cells in *Nitella flexilis*. Later, the term acquired an expanded definition: the time interval between the initiation of successive primordia on the shoot apex (Esau, 1965; Milthorpe, 1956). However, some investigators (Erickson and Michelini, 1957) have attempted to further broaden the definition to include any other stage of development as a reference point (such as, initiation of the leaf, initiation of the bud in the axis of the leaf, or appearance of the leaf tip from the whorl). Hancock and Barlow (1960) suggested the term auxochron as the interval between comparable stages on successive leaves on a stem. This term has seen little use. Bunting and Drennen (1966) proposed the term phyllochron as the interval between appearance of successive leaves on a culm or stem. Scientists in various fields have used all three terms somewhat interchangeably resulting in confusion about the precise definition of each. We suggest that plastochron be defined as the interval between initiation of leaf primordia on the apex and phyllochron as the interval between similar developmental stages of leaves on the same culm. The similar growth stage may be leaf appearance, but it is not restricted to that event. By appearance, we mean visible without magnification, dissection, or changing leaf display.

The phyllochron can be determined in many ways, such as documenting the time of appearance of successive leaves on a culm or measuring the time it takes for an individual leaf to grow. The latter method assumes that a leaf grows within the time of one phyllochron, which may be the case in some species, but not in others. That is, in some species leaf $n + 1$ may appear before leaf n has completed growth. In practice, the Haun scale (Haun, 1973) is often used to determine the phyllochron during vegetative development of grasses and is determined as

$$\text{Haun stage} = [L_n/L_{(n-1)}] + (n - 1)$$

where L_n is the length of the youngest leaf blade above the collar of the subtending leaf, $L_{(n-1)}$ is the length of the blade of the penultimate (subtending) leaf, and n is the total number of leaves that are visible on the culm. By recording leaf lengths and documenting the Haun stage of a culm on at least two dates, the phyllochron can be ascertained by dividing the time interval by the difference in Haun stage on the two dates. As mentioned above, the interval between the events may be measured either in time (hours or days), thermal time (growing degree days [GDD]), or other meaningful measurement of time.

Development and growth of grasses are characterized by the repeated formation, expansion, and subsequent senescence of a basic unit, the phytomer (Gray, 1879). The phytomer is composed of the node and the tissues derived from it—leaf, axillary bud, internode, and in some cases, roots. The papers in this symposium discuss establishment of the phytomer unit and factors influencing growth and further development of the tissues. There is an intrinsic relationship between the concepts of a phytomer unit and the phyllochron. Vegetative growth involves addition of successive phytomer units to the culm. Development can be conceptualized by the addition of successive phyllochron units. Therefore, a phytomer unit, which is the basic building block of grass growth, is added to the culm during each phyllochron.

A number of environmental factors have been reported to affect the phyllochron. Most of the effects of environmental factors are complex. In Table 1, we have simpli-

Table 1. Environmental factors influencing the phyllochron.

Factor	Direction of change in phyllochron with increase in factor†		Citation
Temperature	+	(at high temperatures)	(Masle et al., 1989)
	+	(above the optimum)	(Cao and Moss, 1989)
	+		(Boone et al., 1990)
Nutrient availability	−		(Longnecker et al., 1993)
	0		(Bauer et al., 1984)
	0		(Frank and Bauer, 1982)
Water	0		(Bauer et al., 1984)
	+		(Baker et al., 1986)
Salt	+		(Maas and Grieve, 1990)
CO_2	−		(Boone and Wall, 1990)
Light			
Quantity/ duration	0		(Masle et al., 1989)
	+/0		(Kirby and Perry, 1987)
	−		(Friend et al., 1963)
Quality (more FR)	−	(slight)	(Barnes and Bugbee, 1991)
	0		(Skinner and Simmons, 1993)

† +, increase in phyllochron with increase in factor; 0, no change in phyllochron with increase or decrease in factor; −, decrease in phyllochron with increase in factor. The rate of leaf appearance is the inverse of the phyllochron, and therefore, a decrease in the phyllochron (growing degree days [GDD] leaf^{-1}) results in an increase in the rate of leaf appearance (leaves GDD^{-1}).

fied the reported responses to either a positive, negative, or no change in the phyllochron to an increase in each environmental factor listed. Superoptimal temperatures appear to hasten development (Boone et al., 1990; Cao and Moss, 1989; Masle et al., 1989). Nutrient availability at nonextreme levels seems to have little effect on the phyllochron (Bauer et al., 1984; Frank and Bauer, 1982). However, Longnecker et al. (1993) reported faster development as N was made more available. Water stress also appears to have an impact on phyllochron, but only at extreme levels of stress (Baker et al., 1986; Bauer et al., 1984). Increased salt concentrations (Maas and Grieve, 1990) slowed development by increasing the time for appearance of successive leaves, whereas increased CO_2 concentrations (Boone and Wall, 1990) decreased the phyllochron. In general, light quality, quantitiy, and duration have a minor and varied impact on leaf appearance (Barnes and Bugbee, 1991; Friend et al., 1963; Kirby and Perry, 1987; Masle et al., 1989; Skinner and Simmons, 1993).

The following papers will describe mechanisms of leaf growth, discuss mechanisms by which the rate of leaf appearance is established, describe the variation in the phyllochron found within and among species, relate development of the root system in rice to the phyllochron, compare equations to predict the phyllochron, describe how development stage is used to manage perennial forage grasses, and present a new theory about the relationship between the phyllochron concept and development (from emergence to senescence) in small grains. The papers in this symposium summarized current knowledge about the phyllochron and offered new ideas to advance our understanding of how leaf appearance can be used to understand and predict the timing of phenological events in grasses.

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