

Review Article

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Phyllochron and Tillering Behavior Studies in Grass family (Gramineae): A Review

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The vegetative development in gramineae is characterized by the regular initiation and appearance of successive leaves. Phyllochron is the period of time between the emergence of one phytomer (a set of tiller, leaf, and root which emerges from the base of the plant) and the emergence of next other hands interval between similar growth stages of successive leaves on the same culm, has been used extensively to describe and understand development of rice plant and other grass family. A phyllochron is not a thing but rather a period of time, 5 days at best but usually longer, 12 phyllochrons before the plant begins initiating panicles and starts its reproductive phase. The first tiller off the main stem appears at the fourth phyllochron. The first tiller appeared when the third leaf was completely expanded and the emergence of the fourth leaf tip was initiated in the main stem. The rate of leaf initiation on the apical meristem and the rate of leaf appearance above the pseudostem or whorl are primarily controlled by biotic and abiotic factors that reflect on the growth and yield of crop plants.

Keywords: Phyllochron, leaf initiation rate, biotic and abiotic factor, tillering behavior, productivity.

INTRODUCTION

Phyllochron or leaf emergence rate which has been used to characterize the growth dynamics of cereals is defined as the time interval of leaf emergence [36]. An important plant development parameter is the leaf appearance rate (LAR), which is the number of days required for the emission of one leaf on main culm [49]. Phyllochron or leaf appearance rate an important parameter in the production efficiency of agricultural crops and has been used in ecophysiological studies in plants [46]. 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 [19] is often used to determine the phyllo chron during the vegetative development of grasses and is determined as 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 the Haun stage on the two dates.

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As mentioned above, the interval between the events may be measured either in time (hours or days), thermal time (Growing Degree Days), or another meaningful measurement of time [20]. Leaf development in the mother culm and daughter tiller don't synchronize until the tiller has appeared. As described, the tiller bud is initiated and then, the first leaf emerges in the third plastochrons (time interval between successive leaf initiations) of the mother stem. During this time, the tiller bud produces a total of five foliage leaf primordia. Thereafter, leaf development on each tiller mimics that in the mother stem; tillers and the mother stem share similar phyllochrons and plastochrons. Under unfavorable conditions, many tiller buds become dormant. In such buds, marked decline in growth rate occurs just after they have produced two foliage leaf primordia. Appearance of the tillers (i.e., the emergence of the first foliage leaf from the leaf sheath of its subtending phytomer) is confined to the seventh plastochron [24]. Leaf initiation in rice begins just after seed soaking. Each rice tiller produces 10-18 leaves in its life. Average duration between successive leaf appearances of 4 to 5 days before panicle initiation and 7 to 8 days afterwards [50]. The modeling of the phyllochron was first published in 1951 when Katayama (table 1) presented the growth rules while working leaf emergence on the main stem and tillers of rice, wheat, and barley.

This model was used for explaining the success of the SRI system which he had already developed empirically. When sufficient knowledge had been gained about phyllochron dynamics and the conditions under which rice plants could perform maximally, yield increased as high as 20-30 percent [11]. Studies to determine the phyllochron were performed for crops, such as sorghum [10], brachiaria [40], maize [46], [28], wheat [38], [33] and strawberry [39], [31].

The tillering of these crops depends on the cultivars and resources available for growth and development. On the other hand, excessive tillering lead to high tiller abortion, poor grain setting, small panicle size and finally reduced yield [12]. Higher tiller production has been found to be inversely proportional to the length of phyllochron [48]. Study of the tillering pattern and leaf emergence rate of cereal crops is a crucial need for selection and improvement of productivity. With this, the present review focuses on updating the knowledge about the phyllochron studies and tiller production on cereal crops based on abiotic and abiotic factors so as to increase the productivity level of rice and other gramineae crops.

TABLE 2: Distribution of rural women according to their role & status (n=200)

Phyllochron stage	1 st	2 nd	3 rd	4 th	5 th	6 th	7 th	8 th	9 th	10 th	11 th	12 th	Total
Main stalk		1											1
First row of tillers				1	1	1	1	1	1				6
Second row of tillers						1	2	3	4	5	6	5	26
Third row of tillers								1	3	6	10	15	35
Fourth row of tillers										1	4	10	15
Fifth row of tillers												1	1
Total number per phyllochron	0	1	0	1	1	2	3	5	8	12	20	31	84
Total	0	1	1	2	3	5	8	13	21	33	53	84	

Influence of cultivars on phyllo chron and tillering behavior

The development of the first four leaves on the main stem (period 9-20 days), the phyllochrons was 4.5 days and it was shorter 4.0 days over the 20-29 period, grew longer 6.4 days over the period 38-50 and increased rapidly thereafter (period 50-82 and 82-109 days) corresponding to 12th leaf to heading (15 leaf) in rice variety IR 64 [23]. Phyllochron variability among cultivars was also verified [10], and on wheat [38], barley [37] and strawberry [39]. Different results among cultivars are due to genetic differences. Therefore, the management of these cultivars tends to be differentiated due to the occurrence of variability in leaf development. Moreover, the grower may establish cropping planning for each cultivar with the number of leaves forecast model. There was variability in phyllochron and LAR among cultivars and sowing dates. These differences in phyllochron and LAR observed among cultivars can result from their genetic and physiological differences. Moreover, the differences in phyllochron and LAR among sowing dates can be the result of environmental conditions, mainly the photoperiod [15]. These variations in the LAR estimation among cultivars can be attributed to physiological differences [40]. The TNAU pre-release maize hybrids (CMH 08-282, CMH 08-337, CMH 08-350) produced 22 leaves while private hybrids (NK 6240 and 900 M Gold) produced only 18 leaves (Fig.1 and Fig.2). The highest phyllochron was observed in NK 6240 is 3.98 days and lowest in CMH 08-282 (2.95 days) [43].

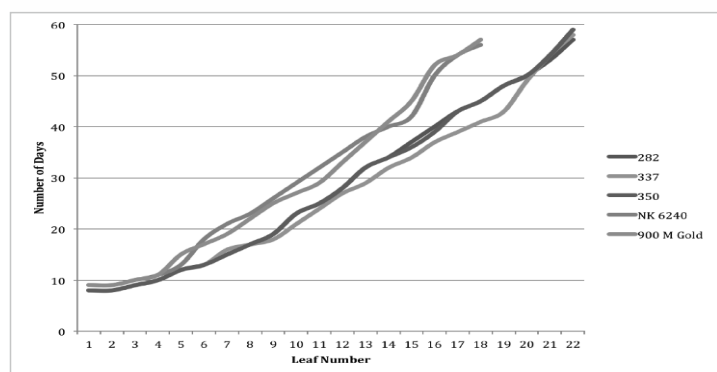


Fig. 1. The effect of phyllochron observed in the five maize hybrids (43)

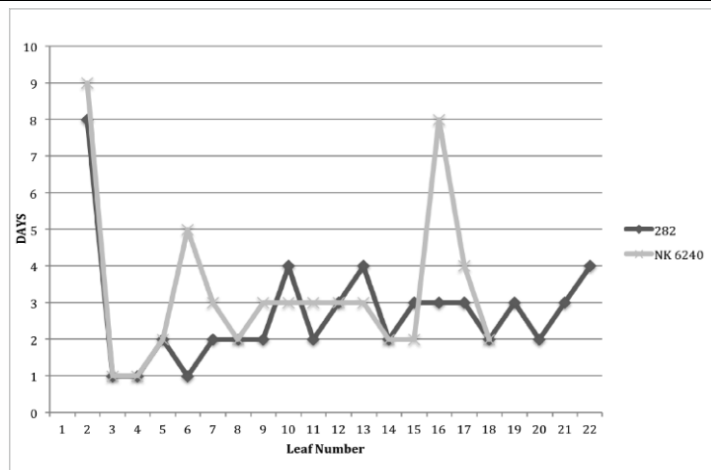


Fig. 2. Number of days taken to emergence of each leaf in CMH 08- 282 and NK 6240 (43)

Influence of age of seedlings on phyllo chron and tillering behavior

Transplanting young seedlings usually from 8 to 12 days and not beyond 15 days old, the exact limit depends on biological processes, measured in terms of phyllochrons [24]; and Nemoto *et al.*, 1995). For maximum tillering, the plant has to complete as many phyllochrons as possible during its vegetative phase [6]. Each tiller produces another two phyllochrons later under favorable growing conditions [44]. When seedlings stay for a longer period of time in the nursery beds, primary tiller buds on the lower nodes of the main culm become degenerated leading to reduced tiller production. When the seed is not planted too deep, tillering starts early in about a fortnight from sowing in case of direct seeding. But, transplanted rice takes little longer time period to start tillering as it first needs more time to recover from transplanting shock. When rice seedlings are transplanted at the right time in terms of age, tillering and growth proceed normally [32].

Irrespective of the nursery techniques the same age of seedling were produced similar phyllochron (table 5) and tillering behavior of rice [4]. Age and number of seedlings had significant effect on phyllochron at 4th, 8th, 9th, 10th and 11th phyllochron in two consecutive years.

Transplanting on 21 days after sowing with one seedling hill⁻¹ took more time (6.6 days) to put-forth of new leaf and was on par with 21 days after sowing with two seedlings hill⁻¹ and 21 days after sowing with three seedlings hill⁻¹ compared to others at 4th phyllochron. At 8th phyllochron 21 days after sowing with three seedlings hill⁻¹ had taken maximum time (5.5 days) and it was comparable with 21 days after sowing with two seedlings hill⁻¹ and 14 days after sowing with three seedlings hill⁻¹. Almost same trend was noted on 9th, 10th and 11th phyllochron [35].

Influence of crop geometry on phyllochron and tillering behavior

The maximum number of tillers produced by the rice plant is inversely proportional to the length of the phyllochron, which is dependent upon the extent of stresses. Wider spacing, availability of solar radiation, medium temperature, soil aeration, and nutrient supply promote shorter phyllochrons which increase the number of tillers in the rice plant [24]. SRI fields will look terrible for a month or more after transplanting, because the plants are so thin and small and widely spaced. In the first month the plant is preparing to the tiller, during the second month, serious tillering begins. In the third month, the field seems to explode with rapid tiller growth. To understand why, you need to understand the concept of phyllochrons, a concept that applies to members of the grass family, including cereals like rice, wheat, and barley [22]. The different types of planting pattern could be modified the phyllochron and tillering behavior of rice (table 2 to 4) [48].

Table 2. Phyllochron observations under square pattern of planting

Phyllochron stage	1 st	2 nd	3 rd	4 th	5 th	6 th	7 th	8 th	9 th	10 th	11 th	12 th	Total
Main stalk		1											1
First row of tillers				1	1	1	1	1	1				6
Second row of tillers								1	2	3	4	5	15
Third row of tillers								1	2	4	5	6	18
Fourth row of tillers										1	3	7	11
Fifth row of tillers												1	1
Total number per phyllochron	0	1	0	1	1	1	1	3	5	8	12	19	52
Total	0	1	1	2	3	4	5	8	13	21	33	52	

Table 3. Phyllochron observations under triangle pattern of planting

Phyllochron stage	1 st	2 nd	3 rd	4 th	5 th	6 th	7 th	8 th	9 th	10 th	11 th	12 th	Total
Main stalk		1											1
First row of tillers				1	1	1	1	1					5
Second row of tillers							1	2	3	4	5	6	21
Third row of tillers								1	2	4	7	10	24
Fourth row of tillers										1	2	5	8
Fifth row of tillers												1	1
Total number per phyllochron	0	1	0	1	1	1	2	4	5	9	14	22	60
Total	0	1	1	2	3	4	6	10	15	24	38	60	

Table 4. Phyllochron observations under oblong pattern of planting

Phyllochron stage	1 st	2 nd	3 rd	4 th	5 th	6 th	7 th	8 th	9 th	10 th	11 th	12 th	Total
Main stalk		1											1
First row of tillers				1	1	1	1	1					5
Second row of tillers							1	2	3	4	5	6	21
Third row of tillers								1	2	5	8	12	28
Fourth row of tillers										1	2	10	13
Fifth row of tillers												1	1
Total number per phyllochron	0	1	0	1	1	1	2	4	5	10	15	29	69
Total	0	1	1	2	3	4	6	10	15	25	40	69	

Plant stand establishment on decreased plant density, the rate of leaf appearance was higher and eventually resulted in the production of 4th and 5th row tillers on the main culm (table 5). This might be the actual reason for production of more tiller with wider spacing, at particular duration and correlated to yield [4].

Table 5. Influence of nursery techniques and crop geometry on Phyllochron of rice

Treatments	3 rd - 4 th	4 th -5 th	5 th -6 th	6 th -7 th	7 th -8 th	8 th -9 th	9 th - 10 th	10 th - 11 th	11 th - 12 th	Total number of phyllochron
Nursery techniques										
N ₁ . Mat nursery	4.3	4.8	4.8	4.4	4.9	4.8	5.2	5.7	8.1	13.3
N ₂ . Wet nursery	4.4	4.9	5.3	4.8	5.2	5.3	4.9	5.8	7.8	13.1
SEd	0.15	0.15	0.30	0.30	0.32	0.23	0.24	0.35	0.39	0.25
CD (P=0.05)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Cultivars										
C ₁ . CORH 3	4.5	5.0	4.9	4.5	4.8	4.8	4.9	5.6	7.9	13.1
C ₂ . ADT 43	4.3	4.8	5.2	4.7	5.3	5.3	5.1	5.8	7.9	13.3
SEd	0.15	0.15	0.30	0.30	0.32	0.23	0.24	0.35	0.39	0.25
CD (P=0.05)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Crop Geometry										
S ₁ . 25 x 25 cm	4.5	5.0	5.3	5.1	5.5	5.8	5.8	6.5	8.1	12.9
S ₂ . 30 x 30 cm	4.3	4.8	5.2	4.6	5.1	4.9	5.0	5.4	8.0	13.3
S ₃ . 35 x 35 cm	4.4	4.9	4.7	4.2	4.5	4.3	4.3	5.3	7.6	13.3
SEd	0.22	0.22	0.30	0.28	0.35	0.34	0.30	0.34	0.30	0.39
CD (P=0.05)	NS	NS	NS	0.59	0.74	0.73	0.63	0.72	NS	NS
Interaction	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

(N₁ & N₂ - 14 day seedlings)

Influence of environmental factors on phyllochron and tillering behavior

Plant growth and development at 20°C and 28°C, linear relations were found between temperature and both the rate of progress towards panicle initiation and the rate of progress towards panicle emergence also found, the rate of leaf appearance was no greater at 28°C than at 24°C. Early transplanting preserves the potential for tillering and root growth that will be lost if transplanting is done after the start of the fourth phyllochron. Phyllochron decreased with increased day length from 124°Cd leaf⁻¹ at 8 h to 97°Cd leaf⁻¹ at 16 hr photoperiod, respectively [13]. Further, the total number of leaves on the main stem decreased at anthesis with increasing photoperiod. The air temperature is the main weather factor that influences leaf development in plant [17]. Phyllochrons decrease with temperature, light intensity, CO₂, and nutrition, whereas it increases with plant density. Humidity has different effects on the phyllochrons, depending on the temperature regime and rate of soil compact ability, seeding depth, vernalization and incident radiation, affect the leaf appearance rate [51]. Permanent cool season grasses and small-seeded cereals, produce one fully expanded leaf each 6-10 days if they are subjected to favorable conditions while, in Maize and warm season cereals, this rate is each 4-6 days [26]. The greater length of leaves in transplanted flooded plants than in aerobic direct-seeded plants may be attributed to the nursery effect. The developmental delay experienced in the nursery accelerates the rate of development after transplanting [9]. NaCl stress may be the reason for low leaf number by inhibiting leaf primordium formation. In the tillering stages of some rice varieties, leaf area indices and leaf area are also inhibited due to the effects of sodium salinity [18].

Table 1. Influence of environmental factors on phyllochron in rice

Factor	Direction of change in phyllochron	Citation
Temperature	+ (above the optimum)	[8], [29]
	-	[26]
Nutrient availability	-	[21],[27], [43]
	0	[5]
Water	0	[5]
	+	[2], [41]
Salt	+	[1], [30], [34]
CO ₂	-	[7], [42]
Light quantity/duration	0	[29]
	+ / 0	[25]
	-	[14]
Light quality	- (slight)	[3]
	0	[45]

(+) means increase in phyllochron with increase in factor,
 (-) means decrease in phyllochron with increase in factor and
 (0) means no change in phyllochron with increase or decrease in factor.

Summary and Conclusions

The present study illustrated that understanding the phyllochron and leaf appearance rate of gramineae. Tillering in a gramineae family has a major determinant for panicle production and as a consequence affects the total productivity. From the foregoing literature, it is concluded that wider spacing invariably promotes higher number of tillers.

On the other hand, closer spacing showed increased conversion efficiency of tillers unit area⁻¹. Existing research focused on alteration of intra-row spaces without altering the inter-row spacing. Decreasing the intra-row spacing levels tends to accommodate more number of plant population unit area⁻¹. Hence, it is integrate the crop geometry, age, number of seedlings and clear view on environmental factors affecting the phyllo chron and leaf appearance rate leading to increased tiller production and productivity of crops.

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