PHYLLOCHRON OF Paspalum notatum FL. AND Coelorhachis selloana (HACK.) CAMUS IN NATURAL PASTURE

Lilian Eggers1*; Mónica Cadenazzi2; Ilsi Iob Boldrini3

1 PUCRS - Dept. de Biologia - C.P. 1429 - 90619-900 - Porto Alegre, RS - Brazil.
2 UDELAR/EEMAC - Dept. de Estatística. Ruta 3, km 363 - C.P. 60000 - Paysandu - Uruguay.
3 UFRGS - Dept. de Botânica, Av. Bento Gonçalves, 9500, prédio 43433, Campus do Vale - 91501-970 - Porto Alegre, RS - Brazil.
*Corresponding author <leggers@pucrs.br>

ABSTRACT: Leaf appearance rate and phyllochron are related variables which play a central role in forage production. Phyllochron is the time interval between the appearance of successive leaves and varies according to a number of environmental factors, among which temperature is the most important. The experiment was conducted in natural pasture with the aim of testing phyllochron variation under different seasons, herbage allowances, and topographic positions. Marked tillers were used to define the phyllochron, establishing a relationship between the number of leaves produced against thermal time during the sampling period. The time (expressed in °C) needed for the emergence of a leaf is equal to 1/b, where b is the slope coefficient of the regression. The lines for the season combinations, herbage allowances and topographic positions sampled were compared. Under Spring and Summer conditions, the phyllochrons for P. notatum and C. selloana were 156°C and 238°C respectively, regardless of treatment.

Key words: morphogenesis, leaf appearance, native grassland

INTRODUCTION

Natural pastures predominate in South Brazil but little is known about morphogenesis of the native species in relation to environmental conditions and grazing pressure. Phyllochron is a morphogenetic characteristic defined as the time interval between the appearance of two successive leaves (Skinner & Nelson, 1995) and it is considered constant when measured as thermal time. In association with other morphogenetic characteristics, it determines the structure of a pasture and its leaf area index (LAI) (Chapman & Lemaire, 1993). Morphogenesis allows the successional dynamics of multispecies pastures to be understood. Through the knowledge of leaf emission rhythm (phyllochron) and characteristics such as extension rate and the rhythm of tillering for different species, associated with the variation in intake (defoliation), it is possible to explain dominance or disappearance of certain species from the community and, consequently, its botanical composition. Phyllochron can be applied in the establishment of mathematical models that can be used by extensionists and producers to determine management practices such as cutting, grazing or application of fertilizers and pesticides (Frank & Bauer, 1989; Wilhem & McMaster, 1995).

The present work tested the hypothesis that there is homogeneity in phyllochron of Paspalum notatum and Coelorhachis selloana plants, sampled in natural pasture, when submitted to factors such as seasons of the year (growth seasons), herbage allowances and topographic...
The lack of knowledge about the basal growing temperature for the studied species prevented the characterization of phyllochron in degree-days (GDD). Therefore the daily temperatures were considered within the range comprised between the basal temperatures for most periods sampled, and thermal time (TT) was calculated for the days under evaluation. TT is the summation of mean daily temperatures, calculated by the arithmetic mean between maximum and minimum daily temperatures, according to the formula: 

\[ TT = \Sigma(T_{\text{max}} + T_{\text{min}})/2 \]

(The analysis was performed using the mixed procedure of SAS application (SAS, 1996). Finally, using homogeneous data set for each species, a single equation was fitted to determine the phyllochron.

During sampling, meteorological variables were monitored and water balance was calculated at 10-day intervals, according to Thornthwaite-Mather. The survey for soil moisture determination was carried out in three occasions (Summer/97; Spring/97; and Summer/98), to characterize the soil moisture in the treatments and to verify the influence of drought periods that occurred during sampling. These data are fully described in Eggers (1999), and will be mentioned here whenever they played a crucial role over the results.

**RESULTS AND DISCUSSION**

*Paspalum notatum*

The phyllochron of *P. notatum* indicated a trend for greater leaf appearance rate (LAR) in the Spring and Summer of 1996/97 (Table 1). The comparison among the
Phyllochron of \textit{P. notatum} and \textit{C. selloana}

Table 1 - \textit{Paspalum notatum} phyllochron, expressed as thermal time/leaf (°C), for the combinations of herbage allowances (HA 4.0, 8.0, and 12.0 kg DM/100 kg LW/day) and topographic positions - TP (Hilltop - Ht; Pediment - Pe), and for all treatments (general) in the seasons of the year (SPG - Spring; SMR - Summer; FALL - Fall), 1996/98.

<table>
<thead>
<tr>
<th>Season</th>
<th>HA × TP</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4 Ht</td>
<td>4 Pe</td>
<td>8 Ht</td>
<td>8 Pe</td>
<td>12 Ht</td>
<td>12 Pe</td>
<td>general</td>
</tr>
<tr>
<td>SPG/96</td>
<td>154</td>
<td>132</td>
<td>156</td>
<td>149</td>
<td>143</td>
<td>192</td>
<td>152</td>
</tr>
<tr>
<td>SMR/97</td>
<td>169</td>
<td>164</td>
<td>159</td>
<td>172</td>
<td>154</td>
<td>169</td>
<td>164</td>
</tr>
<tr>
<td>FALL/97</td>
<td>345 b</td>
<td>222 c</td>
<td>357 b</td>
<td>435 ab</td>
<td>333 b</td>
<td>667 a</td>
<td>345</td>
</tr>
<tr>
<td>SPG/97</td>
<td>164</td>
<td>200</td>
<td>189</td>
<td>217</td>
<td>161</td>
<td>175</td>
<td>182</td>
</tr>
<tr>
<td>SMR/98</td>
<td>159 bc</td>
<td>154 bc</td>
<td>200 a</td>
<td>170 abc</td>
<td>179 ab</td>
<td>143 c</td>
<td>167</td>
</tr>
</tbody>
</table>

For Fall/97 and Summer/98, values followed by a common letter do not differ with regard to the coefficients of the analyzed lines (ANCOVA, $P < 0.05$).

regressions of the HA × TP combinations for each season showed no difference in phyllochron in the Spring/96, Summer/97 and Spring/97.

In the Summer/98, the trend line indicated a phyllochron of 167°C with a coefficient of determination ($R^2$) of 94%. However, treatments differed between extremes of a smaller phyllochron in 12.0% LW, pediment treatment and a greater one in 8.0% LW, hilltop treatment. It is believed that the variation between treatments found for that season resulted from a reduction in the precipitation that occurred in the last two weeks of sampling. Under such conditions, growth response could be different because of the variation in soil moisture content and phyllochron reduction was actually proportional to this variation, corresponding to maximum soil moisture content in 12.0% HA, pediment treatment (14.2%), and minimum in 8.0% HA, hilltop treatment (9.86%) (Eggers, 1999).

In the Fall/97, two factors seemed to have influenced phyllochron increase: the decrease in daily mean temperatures and water deficit period preceding sampling (Eggers, 1999). Regarding temperature, Summer species such as those belonging to \textit{Paspalum} need higher temperatures for growth and development and, although the optimum temperature for \textit{P. notatum} is unknown, it seems that the sampled period (May/97) showed temperatures lower than optimum (mean monthly temperature 15.2°C). Mitchell & Lucanus, quoted by Anslow (1966), investigated the response of different species to temperature regimes and defined the optimum temperatures for leaf appearance in \textit{Paspalum dilatatum} (29 - 35°C), \textit{Lolium perenne} (18 – 29°C), \textit{Agrostis tenuis} (18 – 29°C) and \textit{Dactylis glomerata} (18°C).

The homogeneity among treatments in the Spring/96, Summer/97 and Spring/97 seasons, and the relationship among differences and environment conditions in the Fall/97 and Summer/98 indicated that phyllochron is independent from the HA × TP combinations, what agrees with results reported by Frank & Hofmann (1989), who did not find phyllochron differences among five species submitted to two grazing intensities. On the other hand, Agnusdei et al. (1994; 1996) observed differences in the phyllochron of species subjected to defoliation or under grazing exclusion conditions, and called the attention to the fact that species varies in response. The study on four grasses showed that \textit{Paspalum dilatatum}, differently from \textit{Cynodon dactylon}, \textit{Leersia hexandra} and \textit{Festuca arundinacea}, did not vary in LAR under three grazing conditions (light, moderate, and intense) (Agnusdei et al., 1997).

The similarity between phyllochron in the Spring of 96 and 97 and in the Summer of 97 and 98 (Table 1) allowed the fitness of a general equation for this set of data ($R^2 = 93% ; CV = 14%$), defining a phyllochron of 156°C for \textit{P. notatum} under mild (non-hibernal) temperature conditions and favorable precipitation (no water deficit) (Figure 1). Figure 1 shows the number of leaves produced in all seasons, including Fall/97 and, separately for that, the 4.0% LW, pediment treatment, with similar values observed for all other seasons. The proximity of the 4.0% HA, pediment treatment values in relation to those obtained in the Spring/96, Summer/97 and Spring/97, results from a higher moisture condition in such HA × TP combination, even though specific soil moisture content data are not available for that period.

\textit{Coelorhachis selloana}

The trend lines for the Spring/96, Summer/97 and Summer/98 indicated that \textit{C. selloana} phyllochron was not different in the HA × PT combinations (Table 2). In the Spring/97, phyllochron observed in the 8.0% LW, pediment treatment was smaller than those verified for the hilltop (8.0 and 12.0% LW). The reason for this is not supported by meteorological or soil moisture conditions, and are, therefore, unknown.

In the Summer/97, no differences were verified among HA × TP combinations. However, general phyllochron was 417°C (Table 2), which may be considered very high. It is believed that this could be a consequence of soil water deficit from March to May 97
Phyllochron increase was also observed by Morales et al. (1997) in *Lotus corniculatus* as soil water availability decreased. The phyllochron for this species was 83°C at 100% of the field capacity, increasing to 93°C at 70% and to 110°C at 50% of the field capacity. As a result of the high phyllochron value showed by *C. selloana* in the Summer/97, and the water deficit, those data were discarded for the calculation of the general equation of the phyllochron. Only data from Spring/96, Spring/97 and Summer/98 were used in the regression ($R^2 = 93\%$; CV = 13%), and the phyllochron obtained was 238°C (Figure 2). The effect of water deficit on the appearance of new leaves for this species can be observed in Figure 2 (Summer/97).

Phyllochron in grasses are species-specific and quite variable. In Winter species, such as *Lolium perenne* and *Festuca arundinacea*, intervals of 110 growing degree-days (GDD) and 230 GDD were observed, respectively, between the appearance of two successive leaves (Davies & Thomas, 1983; Lemaire, 1985, quoted by Lemaire & Chapman, 1996). In a greenhouse experiment, a population of *Bromus auleticus* was studied by Soares et al. (1998) and showed phyllochron ranging between 345 and 417 GDD. *Briza subaristata* and *Piptochaetium montevidense* were studied by Denardin (2001), who observed smaller phyllochron in colder periods for both species. According to this author, *Briza subaristata* showed a phyllochron of 244ºC in the Fall and 586ºC in the Summer and, finally, *Piptochaetium montevidense* showed phyllochrons of 320ºC and 555ºC in the Fall and Summer, respectively.

In Summer grasses, the smallest value of phyllochron (84 GD) was recorded for *Pennisetum purpureum* cv. Mott (Almeida et al., 1997). In natural pastures, *Andropogon lateralis* is considered a species with slow emission of leaves, showing thermal time of 392°C for the interval of appearance between two leaves (Cruz, 1998). For the same species, Quadros (1999) obtained a phyllochron of approximately 200 GDD and suggested that the difference with regard to Cruz (1998) was related to a greater nutrient availability in field burning and grazing exclusion treatments studied by him. The *P. notatum* (156ºC) and *C. selloana* (238ºC) phyllochrons lie between the verified for *Pennisetum purpureum* and *Andropogon lateralis* (according to Cruz, 1998). The low phyllochron expressed by *P. notatum* under natural conditions could be considered an indicator of the adaptive advantage of this species in natural fields of the Brazilian state of Rio Grande do Sul, since it represents a species with a high leaf appearance rate. In addition, the prostrate habit and the storage rhizome of this species are favorable in the case of stressful conditions.

Table 2 - *Coelorhachis selloana* phyllochron, expressed as thermal time/leaf (°C), for the combinations of herbage allowances (HA 8.0 and 12.0 kg DM/100 kg LW/day) and topographic positions (Hilltop - Ht; Pediment - Pe), and for all treatments (general) in the seasons of the year (SPR - Spring; SMR - Summer), 1996/98.

<table>
<thead>
<tr>
<th>HA x TP</th>
<th>Season 8 Ht</th>
<th>8 Pe</th>
<th>12 Ht</th>
<th>12 Pe</th>
<th>general</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SPG/96</td>
<td>217</td>
<td>250</td>
<td>222</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td>SMR/97</td>
<td>500</td>
<td>417</td>
<td>526</td>
<td>312</td>
</tr>
<tr>
<td></td>
<td>SPG/97</td>
<td>238 a</td>
<td>185 b</td>
<td>263 a</td>
<td>227 ab</td>
</tr>
<tr>
<td></td>
<td>SMR/98</td>
<td>294</td>
<td>233</td>
<td>250</td>
<td>250</td>
</tr>
</tbody>
</table>

For Spring/97, values followed by a common letter do not differ with regard to the coefficients of the analyzed lines (ANCOVA, $P < 0.05$).

Figure 2 - Relationship between leaf appearance and accumulated thermal time (°C) for *Coelorhachis selloana* in the Spring of 96 and 97, and Summer of 97 and 98.
The determination of phyllochron and the understanding of the influence of environment and management conditions allow a closer observation and analysis of the population dynamics of species of interest in the field. Constancy in phyllochron, based on the evaluation of species in different periods, HA and TP, highlights the crucial role of temperature in the process of formation of new leaves. In addition, a strong influence of water availability was observed. Water availability plays an essential role in cell extension (Schnyder & Nelson, 1988; Skinner & Nelson, 1995) and its decrease reduces extension rate, resulting in longer intervals between the appearance of successive leaves. In this work, a greater phyllochron was observed during periods of water deficit and these observations are consistent with the data of Denardin (2001) who considered that the most limiting factor for vegetative growth in the Summer could be soil water availability rather than high temperatures.

CONCLUSIONS

The phyllochron of *Paspalum notatum* and *Coelorrhachis selloana* did not show differences as a result of the herbage allowances sampled. Differences observed were related to soil moisture conditions in the sampling periods which, together with temperature, are essential aspects influencing phyllochron. In Spring and Summer, considering the absence of water deficit, a constant phyllochron was obtained for each species. Such values find potential application for the validation of prediction models for the structure of a pasture, according to the model proposed by Chapman & Lemaire (1993), and can be used to better define the most suitable moment for the use of management practices.

ACKNOWLEDGEMENTS

To Prof. Dr. Carlos Nabinger for his valuable suggestions and to CAPES for scholarship granted to the first author.

REFERENCES


