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The influence of photoperiod on head formation in some Brachiaria species and Chloris gayana cv. Masaba

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Summary

The effect of the photoperiod on head formation was investigated in 5 *Brachiaria* species and selected ecotypes of *Chloris gayana* cv. Masaba. The experiments were conducted in greenhouses where the grasses were exposed to photoperiods of 10, 12 and 14 h in 1971 and 9, 10¹/₄ and 12¹/₂ h in 1973. The photoperiods comprised 9 hours natural daylight in the summer, supplemented with 40 W incandescent lamps.

It is concluded that *Brachiaria mutica* is a qualitative (obligate) short-day plant whereas *B. ruziziensis* and *Chloris gayana* cv. Masaba are quantitative short-day plants. *B. brizantha* and *B. decumbens* were already flowering when exposed to 24 h photoperiods during the pre-experimental period in 1971. In the *Brachiaria* introduction PI 299498, head formation in both experiments occured a few days earlier under the short photoperiod treatment. In the later-formed heads of all grasses tested the number of racemes per head decreased, though the length of the racemes was not affected. During the 1971 experiment, culm branching was observed in most of the grasses. It was found that in *C. gayana* cv. Masaba 'second-ary' culms were mainly formed during photoperiods of 10 and 12 h but rarely by 14 h. 'Tertiary' culms in *B. ruziziensis* were observed in photoperiods of 10 and 12 h. It is suggested that culm branching can be attributed to high relative humidity.

The low seed production of tropical grasses is mainly caused by the low number of heading tillers per unit area and the disynchronization of the flowering resulting from the long period of head production. It is suggested that more research on the photoperiodic response of these grasses would provide useful information on seed production. After selection of photosensitive cultivars and seed production at latitudes of approximately 15° N and 15° S the long period of heading would be reduced and the synchronization of the flowering would be improved. Some of the

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early heading types of *C. gayana* cv. Masaba are typical examples of photosensitive cultivars.

Introduction

Very little detailed work has been done on photoperiodism in tropical pasture grasses. Broadly speaking, most of these grasses produce heading tillers the whole year round in tropical environments. Reviews by Evans (1964) and Humphreys (1975) reveal that many of these tropical grasses are short-day plants, with only a few grasses flowering when the photoperiod is less than a critical length, while the other species flower more rapidly in short days. These two groups of grasses are called qualitative (obligate) and quantitative short-day plants, respectively. Some tropical grasses such as *Paspalum dilatatum* and *P. notatum* are classified as obligate long-day plants, although in both grasses flowering occurs at latitude 6° N (Surinam). On the other hand Boyce (1970) found that *Setaria sphacelata* cv. Nandi is most probably a quantitative long-day plant. However, the differences in photoperiodic response of one species in different experiments are most probably the result of the particular ecotype or cultivar used and the treatments during the pre-experimental period.

Even in areas with small differences between the shortest and the longest day, the photoperiodic sensitivity of a particular grass can have important consequences on grassland exploitation. For example, in the coastal region of Surinam (6° N; differences in daylength of 43 minutes or less) the pasture grasses *Ischaemum timorense* and *Melinis minutiflora* flower abundantly about December. At that time the stem percentage of the grass crop increases substantially but few young tillers are produced. Consequently the live weight of the grazing animal will fall.

As stem elongation in tropical grasses occurs continuously and abundantly, even in a young growing stage, the leaf percentage in the aging grass crop will decrease rapidly. Thus, the nutritive value of the grass will be greatly reduced, while the dry matter intake of the animal also decreases. At the same time the production of new tillers, which in such a crop situation are also not easily accessible to the grazing animal, will be reduced. Greater sensitivity of tropical grasses to daylength can result in a restricted period of flowering and this will improve the quality of the grass as well as seed production. The next section will deal with this second aspect of the photoperiod.

The role of heading in seed production

Seed yields of tropical pasture grasses are generally very low. Boonman (1971), working with 6 tropical grasses in Kenya, mentioned 7 factors that caused low yields. The most important factors were the number of heading tillers per m², the indeterminate flowering habit and low seed setting of these grasses. However, some of these factors seem to be inherent to the morphological and physiological characteristics of these species. Thus the tiller density of tropical grasses is considerably lower than that of temperate grasses. Consequently, given the same heading per-

centage in both type of grasses, the number of fertile tillers per unit area will be much lower in tropical grasses. This is clearly illustrated in Table 1, where some components of the seed production of tropical and temperate grasses obtained from well managed experiments, are compared. It is evident that the large difference in seed yield between tropical and temperate grasses are mainly the result of the low number of fertile tillers per m². The differences in the number of seeds and the seed weight per inflorescence between the tropical and temperate grasses are almost of the same magnitude within both groups. However it should be noticed that the percentage Pure Germinating Seed (% PGS) of tropical grasses is usually 20-40 whereas it is approximately 90 in temperate grasses.

Seed yields of tropical grasses can be increased by agronomic practices such as nitrogen application and row width, which influence heading. Boonman (1972a, 1972b) conducted experiments on this from 1969 to 1971 (5-6 harvests) with *Setaria sphacelata* cv. Nandi II and *Chloris gayana* cv. Mbarara in Kenya. Data on head numbers and seed yields obtained from different treatments are plotted against each other in Fig. 1. In *Setaria* the highest seed yields (harvested) were attained at 170 heads per m², whereas in *Chloris* they were achieved at approximately 300 heads per m². Boonman (1972a, 1972b) found no significant correlation between head numbers per unit area and average percentage PGS. In *Setaria* the average % PGS was 19.5 whereas 39.7 in *Chloris*. Fig. 1 also shows that an increase in the number of heads resulted in a decrease in seed weight per inflorescence.

It can be concluded from the results quoted that since it is unlikely that the low density of the present assortment of tropical grasses can be improved, higher seed yields will have to be obtained by increasing the number of seeds per head. However, this means improving seed setting. The indeterminate heading habit of these grasses, which are mainly crosspollinating, causes poor synchronization of flowering. This unfavourably affects seed setting, causing it to take place over a long

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Species	Data from*	Fertile tillers per m²	Number of seeds per inflorescence	1000-grain weight (mg)	Seed per inflorescence (mg)	Clean seed (kg/ha)
Setaria sphacelata cv. Nandi II	(1)	40- 278	97 – 224	310 - 340	33 - 75	13 - 99
Setaria sphacelata CPI 32930 and 33452	(2)	5 - 166	50 - 78	833	45 - 65	6 - 39
Chloris gayana cv. Mbarara	(1)	67 - 293	83 - 172	250 - 290	24 - 43	16 - 110
Phleum pratense	(3)	580 - 845	256 - 396	297 - 316	76 - 125	644 - 725
Poa pratensis	(3)	2127 - 2617	109 – 139	219 - 226	25 - 31	522 - 775
<i>Lolium perenne</i> hay type	(3)	1523 - 1958	27 - 32	1490 – 1649	41 - 52	777 - 915

Table 1. Components of seed yields for some tropical and temperate grasses.

* (1) Boonman (1972a, 1972b); (2) Hacker & Jones (1971); (3) Evers & Sonneveld (1954, 1956).



Fig. 1. Relation between number of heading tillers and clean seed yield in Setaria sphacelata and Chloris gayana (data from Boonman, 1972a, 1972b).

period. Consequently, seed shattering occurs particularly in the heads that have emerged early. Roe (1972) estimated that mechanical harvesting can reduce the potential seed yield by more than 40 %.

Naturally the question arises how the indeterminate heading habit of tropical grasses can be reduced. Shortening this period would improve seed setting, and seeds would ripen more uniformly.

Every tiller initiated in a tropical grass is usually able to reach the generative stage after a certain period. As soon as a tiller has reached a certain stage of development or has formed a certain number of leaves, it is receptive to a flower stimulus. The initiation of inflorescence will be determined by daylength, although in tropical grasses low night temperatures can inhibit this process. The different growing stages of the tillers in a grass crop and the slight sensitivity of these tropical grasses to photoperiod prolongs the heading. It has often been said that daylength is unlikely to be an important controlling influence in plants in the tropics, where the range of daylength is slight. However, photoperiodic effects found in *Oryza sativa* and *Sorghum vulgare* (Best, 1961; Keulemans, 1959) suggest that the small seasonal changes in tropical daylengths may have marked effects on inflorescence initiation.

To gain a better insight into the sensitivity of tropical grasses to daylength an experiment was conducted with some *Brachiaria* species and *C. gayana* cv. Masaba material.

Material and methods

The first experiment was conducted in the summer of 1971 in temperature-controlled greenhouses. The grasses included were: *Brachiaria brizantha* (Hochst.) Stapf, *B. decumbens* Stapf, *B. mutica* (Forsk.) Stapf, *B. ruziziensis* Germain et Evrard, B. species P.I 299498 USDA and *Chloris gayana* Kunth.

The *Brachiaria* species were introduced from Surinam where these grasses have been propagated vegetatively for many years to establish pastures. The introduced material consisted of a few splits and is therefore of a narrow genetic constitution. The *C. gayana* material was selected from the Masaba Foundation Field of the National Agricultural Research Station, Kitale, Kenya (Boonman, 1977). The introductions included splits (clones) and seed material and was described as follows in Kenya:

Clone 1 (C1)	-	very leafy,	early	heading t	ype with	200-250	heads	per m ² ;
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- Clone 2 (C2) leafy, early heading type with 150-200 heads per m^2 ;
- Clone 3 (C3) leafy, medium-late heading type with 150-200 heads per m^2 ;
- Seed 1 (S1) harvested from a leafy, late heading type with 100-150 heads per m²;
- Seed 2 (S2) harvested from a leafy, late heading type with 50-100 heads per m²;

The interval between early and medium-late heading types was 2-3 weeks in Kenya whereas the interval between early and late heading types was 4-5 weeks. Starting from April 1971 the plant material of the *Brachiaria* species was vegeta-tively propagated in sand-filled 5-litre plastic pots (300 cm² surface area). The day and night temperatures prior to the start of the experiment were 29 °C and 23 °C respectively. During this period the plants were exposed to a photoperiod of 24 hours, obtained from artificial illumination.

Repeated stem cuttings were made from the *C. gayana* clones starting from February. The seed material was sown in wooden trays and the seedlings were transplanted 10 days after germination. Multiplication was encouraged by providing day and night temperatures of 25 and 20 °C respectively and a daylength of 24 h. Mid-April all plants were transplanted to 5-litre plastic pots and kept for one month in a phytotron with 16 h photoperiod. From mid-May to the start of the experiment (28 June) the material was again kept in the greenhouse under a daylength of 24 h.

During the pre-experimental period all grasses were regularly treated with a complete solution of minerals, and clipped to a height of 25 cm. The average radiation (400-10 000 nm) inside the greenhouse during May and June was 1377 J cm⁻² day⁻¹. The experiment was started on 28 June, when 2-4 pots of each grass or clone were exposed to photoperiods of 10, 12 and 14 h. The photoperiods were made up of 9 hours natural light from 08.00 until 17.00 and supplemented with low intensity light from incandescent lamps (40 W) for 1, 3 and 5 h respectively. The average radiation inside the greenhouse during the period from 28 June to 20 September was 1046 J cm⁻² day⁻¹. The average relative humidity was about

70 % during the day and 75 % at night.

During the experiment, newly produced heading tillers in at least two pots per treatment were marked with a label showing the date. The appearance of the head through the flag-leaf was used as criterion for heading. The number and the length of the racemes of certain heads were recorded and in the *Brachiaria* species the number of spikelets per raceme was also counted.

Results and discussion

The results of the *Bracharia* species and *Chloris gayana* will be presented seperately. The former are all different species whereas the latter are selected types of the Masaba variety of Rhodes grass.

Bracharia species

After a long pre-experimental period (daylength of 24 h) the development of *B. brizantha* and *B. decumbens* was already so far advanced that no influence of photoperiod on heading could be expected. At termination date (after 37 days) the same number of heads was counted in both grasses in all three photoperiod treatments. Furthermore the heading curve was similar for both *Brachiaria* spp. However reactions to different photoperiods were very evident in *B. ruziziensis*. Initial heading was stimulated by the 10-h treatment and was also accelerated in the short-day treatments. However, the number of heads per unit area was approximately the same for all treatments at the respective termination days. Fig. 2 presents the cumulative heading curves of these three *Brachiaria* species.

B. mutica did not produce heads in the 14-h treatment, but shortening the photoperiod from 12 h to 10 h resulted in earlier and somewhat accelerated heading. In *Brachiaria* sp. PI 299498 heading had already occured 10 days after the experiment had commenced. In this grass the first heads were produced a few days earlier in the short-day treatments. At termination date (after 43 days) the number of



Fig. 2. Cumulative heading curves of three *Brachiaria* species subjected to different photoperiods (---B. *brizantha* and *B*. *decumbens* (10, 12, 14 h); -B. *ruziziensis*).

Species	Date	Number of racemes per inflorescence	Length per raceme (cm)	Spikelets per cm	Spikelets per raceme	Spikelets per inflorescence
B. brizantha	19 July 1971	5.3	7.0	3.4	24	127
	3 Aug. 1971	3.9	8.4	2.9	24	94
B. decumbens	19 July 1971	3.5	6.9	4.4	30	105
	3 Aug. 1971	2.6	7.2	4.2	30	78

Table 2. Some characteristics of the inflorescences of B. brizantha and B. decumbens at different dates (averaged from 3 photoperiods).

heading tillers in the 14-h treatment was half that produced in each of the 10-h and 12-h treatments.

In order to confirm the above results an experiment was repeated in 1973 with photoperiods of 9 h, $10\frac{3}{4}$ h and $12\frac{1}{2}$ h. The experiment was started mid-May and terminated at the end of July (an experimental period of 77 days). During this experiment the average radiation inside the greenhouse was 1235 J cm⁻² day⁻¹. Average day and night temperatures during the treatment period were 33 and 25 °C respectively. The grasses were in a younger growing stage at the start of the experiment than was the case in 1971. Only the time of heading was recorded. The reactions of *B. brizantha* and *B. decumbens* to different photoperiods were similar to the results found in 1971. In both grasses and in all photoperiod treatments the first heads were observed 14 days after the start of the experiment. However, the 9-h photoperiod tended to accelerate heading. Shortening the daylength resulted in an increase in the number of heads in *B. decumbens*, whereas in *B. brizantha* the same number of heading tillers was present in all photoperiodic treatments at termination date.

In *B. ruziziensis* the emergence of the first heads occured later in the $12\frac{1}{2}$ -h treatment than in the two shorter photoperiods. In addition, at termination date it was found that the shorter the daylength had been, the more heading tillers had been produced (181 heads per pot in the 9-h treatment compared with 100 heads per pot in the $12\frac{1}{2}$ -h treatment). This clearly shows that *B. ruziziensis* is a quantitative short-day plant. In experiments conducted to study the influence of daylength on the nutritive value of *B. ruziziensis* it also appeared that shortening the daylength from 16 h to 12 h accelerated heading (Deinum & Dirven, unpublished results). This agrees with results from Puerto Rico (Vicente-Chandler et al., 1974) where *B. ruziziensis* flowers abundantly during the late autumn.

Heading showed a marked response to daylength in *B. mutica*. In the $12\frac{1}{2}$ -h treatment no heading tillers were produced, whereas the number of heads in the 9-h treatment at termination date was considerably higher than that in the $11\frac{3}{4}$ -h treatment. *B. mutica* should therefore be regarded as a qualitative (obligate) short-day plant and at higher latitudes in the tropics will form its heading tillers in the late autumn.

In Brachiaria sp. PI 299498, initial heading started in the shortest daylength, as

was found in 1971. However, the total number of heads at termination date varied markedly in all three treatments.

A number of characteristics of the inflorescence were measured in 1971. Since there were no significant responses to photoperiod in *B. brizantha* and *B. decumbens* the data obtained from the early and late heading tillers of all three treatments have been averaged and summarized in Table 2. In both grasses there were more racemes per inflorescence in the heads that had been produced by 19 July, but the racemes of the later heads were longer.

The number of spikelets per cm decreased in the later-produced heads but the total number of spikelets per raceme was the same in both the early and late heading tillers, indicating some kind of compensating process. This contrasts with the results of Boonman (1972b) who found fewer and shorter racemes per head in later produced inflorescences of *Chloris gayana* cv. Mbarara. However, his results were obtained from field trials in Kenya whereas our data are from pot experiments in greenhouses.

In both *Brachiaria* spp. there were 26 % fewer spikelets per inflorescence in the late heading tillers. In *B. ruziziensis*, short days (10 h and 12 h daylength) appeared to reduce both the number of racemes per inflorescence and the length of the racemes of the late heading tillers. However, no such differences in the raceme characteristics of early and late heading tillers were found in the 14-h treatment.

Potential seed yields can be calculated from the data obtained from the *Brachiaria* species studied. Under field conditions assuming 400 heading tillers per m², 100 spikelets per inflorescence and a 1000-grain weight of 1930 mg it is possible to calculate a seed yield of 772 kg/ha for *B. ruziziensis*. In Kenya, Boonman & van Wijk (1973) obtained an average PGS yield of 23 kg/ha in this grass (a recovery of 3 %). In *Setaria sphacelata* Hacker & Jones (1971) reported a calculated recovery of the potential seed yield of 5-7 %.

In both experiments (1971, 1973) we observed the phenomenon of culm branching in B. brizantha and B. decumbens. In B. ruziziensis 'tertiary' culms were even noticed. 'Secondary' culms develop out of elevated nodes in the parental culm and are able to form inflorescences. Boonman (1971b) noticed this phenomenon in Panicum coloratum and Setaria sphacelata cv. Nandi in Kenya. In Surinam culm branching has also been observed in P. coloratum and B. decumbens. In the Netherlands this phenomenon was noticed as early as 1919 by Hessing in Lolium multiflorum Lamk. and by ten Rodengate Marissen (1923) in Panicum miliaceum and Phalaris canariensis during rainy summers. The culm branching in our experiment was most probably caused by high relative humidities and an optimal supply of nutrients. The highest numbers of 'secondary' culms per parental culm counted in B. brizantha, B. decumbens and B. ruziziensis respectively were 4, 2 and 7. In the latter grass a maximum of 6 'tertiary' culms was observed. On average, the period between the heading of the parental and 'secondary' culms was 14 days. However, in some tillers of B. ruziziensis this period was only two days. 'Tertiary' culms were observed in this grass approximately 14 days after the appearance of 'secondary' heading tillers. The sequence in which the nodes of the parental tiller produced 'secondary' culms was very variable. However, the 'tertiary' culms were



Fig. 3. Effect of three photoperiods on the heading of the total *Chloris gayana* cv. Masaba material.

always observed first at the top node of the secondary' culm. The average number of racemes per head decreased from 'primary' to 'tertiary' heading tillers, but in all types of heads, raceme length was approximately the same.

Chloris gayana cv. Masaba

Before the start of the experiment the numbers of tillers per pot in each treatment was counted. Microscopic analysis of several growing points of the shoots before the experiment began revealed that all the grasses were still vegetative. Recording of the 10-h, 12-h and 14-h treatments was terminated on 6, 10 and 20 September 1971, i.e. 70, 74 and 84 days respectively after the start of the experiment.

The influence on the 3 photoperiods on the heading of all the material (clones + seed) is summarized in Fig. 3. It is evident from the curves that an increase in the photoperiod results in a marked delay in initial heading. In addition, Fig. 3 clearly shows that the total number of heads per pot is highest in the 10-h treatment.

It is of interest to note that in the 10-h photoperiod treatment 65 % of the heading tillers recorded at termination date were already present after 3 weeks; obviously this improves the synchronization of flowering and consequently results in higher seed yields.

The curve of the 12-h photoperiod echoes that of the 10-h photoperiod, but at a lower level. In the 14-h treatment the decrease in heading is spectacular. In view of the selection of flowering time and head density in the Masaba foundation field in Kenya it was anticipated that there would be differences in photoperiodic reac-

Length of photoperiod (h)	10	12	14
Duration of experiment (days)	70	74	84
C1	114	96	46
C2	122	75	33
C3	88	56	15
S1		37	0
S2		41	0

Table 3. The number of heading tillers of different clones and seed material of *Chloris gayana* cv. Masaba subjected to 3 photoperiods, expressed as percentages of the number of vegetative tillers present at the start of the experiment in 1971.

tion. At the start of the experiment there were some differences between the number of tillers per pot of the clones and the seed material. Therefore the number of heads at termination date were expressed as percentages of the total number of tillers (Table 3).

The differences in number of heads produced by the different clones and seed material used in this experiment were similar to results found in the Masaba foundation fields in Kenya (Boonman, 1977). The number of heads produced was found to decrease in sequence from C_1 to S_2 and this was accompanied by a delay in flowering and a lower head density per m². In our experiment increase in photoperiod produced a decrease in heading in all materials. No heading tillers were produced in the plants obtained from seeds (S_1 and S_2) that were subjected to a photoperiod of 14 h. The differences between clones were more pronounced as photoperiod was lengthened.

From these results it was concluded that *Chloris gayana* cv. Masaba is a quantitative short-day plant. However, the reaction of the grass to a daylength between 10 and 12 h was still unclear and it was not certain that heading would be delayed in photoperiods shorter than 10 h. Therefore, a similar experiment was repeated in 1973, but only clones 1, 2 and 3 were exposed to photoperiods of 9, $10\frac{2}{3}$ and $12\frac{1}{2}$ h respectively. The experiment was conducted under the same growing conditions already described for the *Brachiaria* spp. in 1973. However, at the start of the experiment the grasses were in an earlier growing stage than was the case in the 1971 experiment. In Table 4 the total numbers of heads per pot at termination date (after 77 days) are summarized.

There were no significant differences in photoperiodic response between the

Table	4.	The	number	of	heading	tillers	per	pot	of	3	clones	of	Chloris	gayana	cv.	Masaba
subject	ted	to th	ree phot	ope	riods in 1	1973.										

Clone	Photoperiod length (hours)							
	9	10 3	12 1					
C1	55	53	0					
C2	35	43	1					
C3	35	36	4					

photoperiods of 9 and $10\frac{3}{4}$ h. As was found in 1971, clone 1 produced the highest number of heads; this corresponds with van Soest's (1973) findings at Kitale, Kenya (1° N). The time of initial head emergence decreased in sequence from clone 1 to clone 3. After approximately 40 days the percentage of total tillers that had heads was 43 %, 22 % and 5 % for clones 1, 2 and 3 respectively. This was calculated in using the mean of the tillers from the 9-h and $10\frac{3}{4}$ -h treatment. Some days before the termination of the experiment a few heading tillers were observed in the $12\frac{1}{2}$ -h photoperiod: the young growing stage of these plants at the start of the experiment may have delayed their photoperiodic introduction.

In the 1971 experiment the number of racemes per head in the 10-h and 12-h treatments decreased in later-formed heading tillers. Boonman (1972b) found the same phenomenon in C. gayana cv. Mbarara. However this was not found in the 14-h treatment and may therefore be ascribed to the delayed heading which resulted in a higher total light intensity for the tillers.

The phenomenon of culm branching already found in the *Brachiaria* species was also observed in *C. gayana* cv. Masaba. The number of 'secondary' culms that elongated from the main tiller varied from 1 to 7. The sequence in which the nodes of the parent tiller formed 'secondary' culms was very variable. There were fewer racemes per head in the 'secondary' heads than in the 'primary' heads. The length of the racemes of both types of heads did not differ significantly.

Conclusion

It is a fact that the low seed production of tropical pasture grasses is mainly due to the low number of fertile tillers per unit area. This is a direct consequence of the low tiller-density of tropical grasses. However it is unlikely that tiller-density can be improved, and therefore higher seed yields will only be obtained if more seeds are formed per inflorescence. The prolonged head emergence of these grasses, however, results in a disynchronization of flowering and there is a need for more photosensitive cultivars that have a restricted flowering period. The results of our experiments indicate that *Brachiaria mutica* is a qualitative (obligate) short-day plant whereas *B. ruziziensis* and *Chloris gayana* cv. Masaba are quantitative shortday plants. This latter variety of Rhodes grass has early and late heading types in Kenya which show marked differences in photoperiodic response.

It is suggested that to improve the seed yields of tropical grasses, such photoperiod-sensitive cultivars should be cultivated in areas with pronounced differences in daylength during the growing season. The length of the shortest day in the winter at latitudes 23° N and 23° S is approximately $10\frac{1}{2}$ h, whereas that of the longest day in the summer is $13\frac{1}{2}$ h. However, near these latitudes the winter temperatures are too low to grow tropical grasses successfully. It may therefore be advisable to commence commercial seed production of these types of grasses at latitudes of approximately 15° N and 15° S. By carefully choosing the time when the cleaning cut is made, a restricted period and synchronization of flowering can be achieved, which will result in higher seed yields.

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