Netherlands Journal of Agricultural Science 35 (1987) 21-28

The effect of tiller length and age on herbage quality of hybrid pennisetum canopies

M. Warndorff [1], A. Dovrat [1] and T. Kipnis [2]

[1] Faculty of Agriculture, Hebrew University, P.O. Box 12, Rehovot 76-100, Israel
[2] Volcani Centre, Agricultural Research Organization, P.O. Box 6, Bet Dagan, Israel

Received 28 August 1986; accepted 18 November 1986

Key words: Pennisetum americanum P. purpureum, leaf blades, stem+sheaths, whole tiller, IVDMD, in vitro digestibility.

Abstract

Whole plants were sampled every one-and-a-half weeks from field-grown hybrid pennisetum (*P. americanum* × *P. purpureum*) canopies which were cut at intervals of 3 or 6 weeks. Tillers of varying lengths were analysed for in vitro dry matter digestibility (IVDMD). During the 6-week growing period the average whole-tiller digestibility decreased and the difference in digestibility between tillers of different lengths became smaller. In the 42-day old herbage, no difference in IVDMD was found between tillers 10 or 70 cm tall. Separate analysis of stem+sheaths and leaf blades digestibility showed that stem+sheaths digestibility consistently decreased with tiller length, but that digestibility of leaf blades, behaving like stem+sheaths, for 21 days, was positively related to tiller length in 31- and 42-day old herbage. In addition, when comparing tillers of similar length at different herbage ages, it was found that both leaf blades and stem+sheaths digestibility decreased with time.

The average digestibility of the herbage from the 3-week cutting interval at day 21 was lower than herbage of the same age of the 6-week cutting interval. This difference was attributed to the morphologically more advanced canopy after the 3-week cutting interval, due to the difference in the mode of re-growth, which was conducive to faster shoot production as well as to an increase in the percentage of higher insert leaves in the 3-week compared with the 6-week cutting interval.

It was concluded that mainly two factors caused the decline of the whole-herbage digestibility with time, on the one hand the appearance of tall-stemmed tillers, and on the other the deteriorating effect of low light intensities on the tillers growing deeper in the canopy. These results suggest that it is doubtful whether tiller length or other morphological or physiological parameters can be used in grasses to predict herbage digestibility, unless the effect of different light intensities in the ca-

nopy on the digestibility of the various plant fractions can be quantified. Results also suggest that breeding for better digestibility by selection for higher stem digestibility is more promising than for reduced stem growth.

Introduction

In hybrid pennisetum, as in grasses generally, forage quality deteriorates with age (Muldoon & Pearson, 1977). This deterioration is associated with stem formation resulting in a lowering of the leaf/stem ratio, as well as with a steady decline in digestibility of both leaf and stem material (Deinum & Dirven, 1971; Hacker & Minson, 1981; Wilson & Wong, 1982.) Thus, the digestibility of a forage canopy could possibly be predicted from the morphological stage of development of the tillers.

However, a forage canopy is composed of tillers of diverse age and morphological development. Therefore an accurate method for predicting herbage quality from the stage of development of the tillers needs to take into consideration the relative proportion of tillers (number or weight) belonging to different stages of development (Kalu & Fick, 1981).

In a previous paper we reported on a model for the prediction of re-growth and yield of hybrid pennisetum (Warndorff et al., 1985). To that purpose the tillers of the canopy are divided into different length classes and the number and weight of tillers in each class are calculated for each day of growth. If an index relating digestibility to tiller length was available, the canopy structure data generated by the model could then be used to calculate the digestibility of the predicted yield.

The purpose of this study was to investigate the relationship between the length and the digestibility of tillers from hybrid pennisetum canopies differing in age and morphological structure, and to assess the possibility of predicting herbage digestibility from tiller composition.

Materials and methods

Details of the experiments from which the herbage samples were collected for determining IVDMD have been previously reported (Warndorff et al., 1985). Briefly, 6 m × 12 m plots of hybrid pennisetum (*Pennisetum purpureum* × *P. americanum*) cv. N23 × 23A, with plants equally spaced at a density of 2.4 m^{-2}, were cut to a 10 cm stubble at either 3- or 6-week intervals during a period of 130 days in summer. The climatic conditions during this period were uniform.

Every 10 or 11 days one plant, randomly chosen from each of the 6 replicate plots per treatment, was cut at 10 cm above the soil surface, weighed green, and the total number of tillers counted. Approximately one-third of the plant was taken for determining the percentage of dry matter. The remainder was analysed as follows: (1) the length of each tiller was measured from the cutting level to the ligule of the youngest fully expanded leaf, and (2) the tillers were then graded by length into classes and counted.

Tillers of an identical class from the 6 replicate plants per treatment were merged

in equal parts and used to determine the following parameters: (a) dry weight of leaf blades per tiller, (b) dry weight of stem+sheaths per tiller, and (c) IVDMD of leaf blades and of stem+sheaths.

Presentation of the distribution of shoot weight among the different tiller classes is simplified by using only 4 groups obtained by summing the contents of individual classes: tillers smaller than 10 cm, from 10 to 20 cm, from 20 to 40 cm and longer than 40 cm. Samples for IVDMD analysis of 21-day old herbage were taken from 3 cycles (out of six of the 3-week cutting interval treatment), and of 21-, 31- and 42-day old herbage from 3 cycles of the 6-week cutting interval treatment.

Samples selected for IVDMD determinations were of the following tiller classes: 5-10, 15-20, 25-30, 45-50 and 60-70 cm long. These classes were chosen because of their availability from the different treatments at all stages of the experiment.

IVDMD determinations were carried out according to the two-stage in vitro technique of Tilley & Terry (1963), and standardized by means of samples of known IVDMD values.

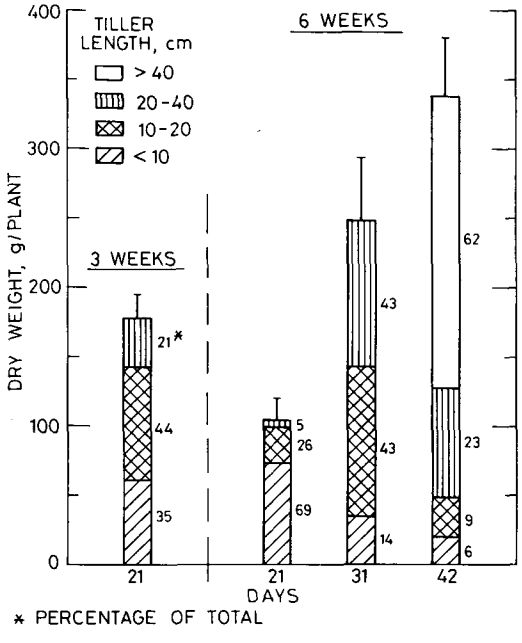

Fig. 1. Effect of herbage age and cutting interval on dry weight per plant and distribution of tillers of different lengths of hybrid pennisetum. Means of six 3-week and three 6-week cutting intervals (vertical bars represent standard errors of the means of total dry weight). Number of plants 2.4 m^{-2}.

Results

Canopy structure and growth

Change in the structure of the canopies during growth is shown as the distribution of plant weight among the different tiller classes (Fig. 1). After 21 days of regrowth at the 6-week cutting interval most of the plant weight was from tillers < 10 cm height, but by 42 days these small tillers comprised only 6 % of plant weight and tillers > 40 cm gave most (62 %) of the yield.

Cutting interval markedly affected plant structure as seen by comparison of tiller size distribution at day 21 in Fig. 1. The plants of the 3-week cutting interval were morphologically more advanced than those of the 6-week interval. Weight per plant of the 3-week cutting interval was about 80 % greater and more of the plant weight was in the taller tillers.

Tiller digestibility

Whole-tiller digestibility of the 6-week interval treatment averaged circa 71 % in the 21-day old regrowth (Fig. 2), IVDMD being 5 units higher for the smallest tillers. In the 31-day old herbage average IVDMD of the tillers had fallen to 67 % and the trend in IVDMD between tiller sizes was reversed, namely the digestibility of tall tillers was higher than of small tillers. At day 42 the mean tiller digestibility decreased to approximately 60% and no relationship was found between tiller length and IVDMD (Fig. 2).

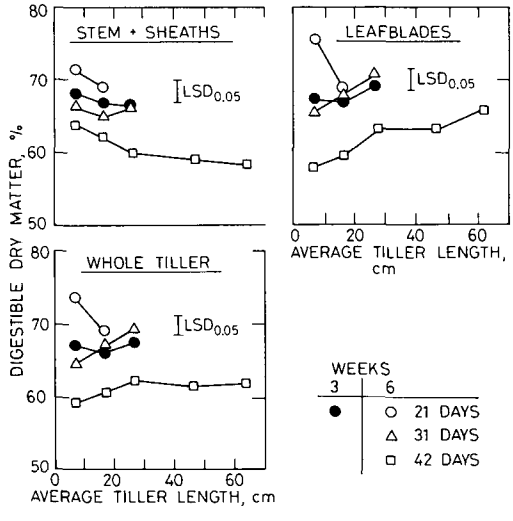

Fig. 2. Effect of herbage age, tiller length and cutting interval on IVDMD of stem+sheaths, leaf blades and whole tillers (weighted for leaf blades/stem+sheaths ratio) of hybrid pennisetum. Means of three 3-week and three 6-week cutting intervals.

Separate analysis of leaf blades and stem+sheaths, however, revealed a distinct relationship between tiller length and IVDMD. In general, the stem+sheaths IVDMD was negatively related to tiller length, i.e., the taller the tiller, the lower stem+sheaths digestibility. On the other hand, leaf blades digestibility, in the younger herbage decreasing with tiller length, was positively related to tiller length in the 31- and 42-day old herbage. At the same time it should be noted that the digestibility of both leaf blades and stem+sheaths declined with herbage age, even when tillers of the same size were compared.

The 21-day old herbage of the 3-week interval was characterized by relatively little variation in digestibility between the tiller classes, regarding both stem+sheaths and leaf blades. The mean digestibility of the 21-day old herbage (67 %) was similar to that of the 31-day old herbage of the 6-week interval.

In both cutting interval treatments the digestibility of leaf blades was usually higher than that of stems+sheaths except in the case of small tillers in the 42-day old herbage of the 6-week cutting intervals.

Discussion

Although the average IVDMD of the various tiller classes (Fig. 2) does not accurately represent total herbage digestibility, since not all classes were analysed, it is safe to conclude that with time herbage weight increased but digestibility decreased. The average IVDMD of about 60 % for the 42-day old herbage corresponds well with values reported for hybrid pennisetum by Muldoon & Pearson (1977) and Hanna & Monson (1980).

The decline of digestibility of the plants with age was not only associated with the appearance of taller tillers of lower digestibility, which is the explanation mostly given (Deinum & Dirven, 1971; Wilson & Minson, 1980), but was also due to the low digestibility of leaf blades of the smaller tillers (Fig. 2). If similar observations have yet not been reported, it probably is because the smaller tillers are only a relatively small fraction of the total herbage of an aged canopy, and these small tillers are likely not to be sampled.

Causes of deterioration in quality which occurs with the increase in tiller size are usually associated with the lower digestibility of the new high-insertion leaves and the deterioration with ageing of the older low-insertion leaves (Deinum & Dirven, 1971; Deinum, 1976; Wilson, 1976). Furthermore, the increased lignification of the stem, especially the upper internodes (Pritchard et al., 1963), and the lower leaf/stem ratio of the taller tillers (Deinum & Dirven, 1971; Muldoon & Pearson, 1977) may take their toll. Under constant environmental conditions, therefore, a consistent negative relation between tiller length and digestibility is to be expected. The unexpectedly low IVDMD values of the small tillers, as was found in the 6-week interval (Fig. 2), therefore could be related to conditions other than age.

With re-growth after defoliation the foliage rapidly increased in size, absorbing more and more of the incident light. The first tillers to grow after defoliation received full sunlight, while those developing afterwards were mostly found in the shade of the older tillers. New leaves which appear under low light conditions exhibit

reduced photosynthetic activity (Woledge, 1978), and have a lower digestibility than comparable leaves which are not shaded (Wilson & Wong, 1982).

Shading to 40 % of natural light intensity reduced whole-herbage digestibility of maize through increasing the relative proportion of the less digestible cell-wall contents (Struik, 1983). With green panic, under comparable conditions, the percentage of cell-wall contents decreased, but overall digestibility was reduced, associated with a lower total soluble carbohydrate content, higher lignification, and possibly reduced cell-wall digestibility (Wilson & Wong, 1982).

In whatever manner, it seems likely that the low digestibility of the small tillers in the 42-day old herbage was due to the effect of shading. This conclusion is supported by the fact that leaf blade digestibility in the 31- and 42-day old herbage increased with the length of the tiller. Additional evidence is the high proportion of dead tillers found in the smallest tiller classes, the proportion of which decreased with tiller length and increased with herbage age (Warndorff et al., 1985). Ong (1978) found that subjecting grass plants to acute shading stress results in tiller death, occurring primarily in the smallest or youngest tillers.

The results of the 3-week cutting interval illustrate the effect of the length of the cutting interval on canopy structure and tiller digestibility. While only 21 days old, the average IVDMD at the 3-week cutting interval was similar to that of the 31-day old herbage at the 6-week cutting interval. Obviously part of the cause of the relatively low digestibility of the 3-week cutting interval was that its canopy structure was morphologically more advanced (Fig. 1), resulting from the different mode of regrowth after defoliation (Warndorff et al., 1985). An additional explanation for the lower digestibility could be related to the findings of Wilson (1976), who predicted that primary growth from seed would be more digestible than from re-growth, as the latter contains more leaves of higher insertion levels. Although in this experiment re-growth occurred after both cutting intervals, an important distinction should be made between them on the basis of the source of re-growth. The regrowth after the 6-week cutting interval originated from new basal buds which may be equated with primary growth, whereas the re-growth after the 3-week cutting interval contained a high proportion of tillers which continued elongation after defoliation (Warndorff et al., 1985).

The results from this study suggest that it is not likely that herbage IVDMD from tiller composition of a hybrid pennisetum canopy can be predicted when tiller length is used as a sole index of digestibility. This is probably true for other grasses but not for legumes since low light intensities possibly do not have the same deteriorating effect on the digestibility of legumes as they have on grasses (Wilson & Wong, 1982). Therefore with legumes, the classification of shoots based on morphological or physiological parameters is more likely to be suitable for predicting digestibility. Kalu & Fick (1981) with lucerne have already obtained some positive results in this respect.

Because of the low digestibility values obtained from tall stems of tropical grasses, it has been suggested that by preventing stem elongation higher digestibilities could be expected (Wilson & Minson, 1980). In the light of the above findings this conclusion may be queried. Preventing stem elongation creates a low-light environ-

ment for most leaves, and we suggest that the lower digestibility of short tillers may be due to this shading. Secondly, without stem elongation the proportion of defoliated tillers which re-grow and contribute only higher-insert leaves, would be increased. Breeding for more digestible stems would be a more promising alternative than preventing stem elongation.

In conclusion, our original hypothesis that tiller digestibility is related to its physiological age as expressed by its length had to be abandoned, and with it the hope of being able to predict herbage quality when the distribution of plant weight among different tiller developmental classes is known. The influence of an additional factor, presumably light, was unexpectedly large, and seems to be of similar magnitude as the known effect of tiller size on digestibility. This information may be of significance for the breeding of tall grasses with higher forage quality and for the development of predictive models of herbage quality.

Acknowledgement

This research project was supported by a grant from the US-Israel Agricultural Research and Development Fund (BARD).

References

Deinum, B., 1976. Effect of age, leaf number and temperature on cell wall and digestibility of maize. In: Carbohydrates in plants and animals. *Miscellaneous Papers* 12, Agricultural University, Wageningen.

Deinum, B. & J. G. P. Dirven, 1971. Climate, nitrogen and grass. 4. The influence of age on chemical composition and in vivo digestibility of maize *(Zea mays* L.) and tall fescue *(Festuca arundinacea* Schreb.). *Netherlands Journal of Agricultural Science* 19: 264-272.

Hacker, J. B. & D. J. Minson, 1981. The digestibility of plant parts. *Herbage Abstracts* 51: 459-482.

Hanna, W. W. & W. G. Monson, 1980. Yield, quality and breeding behavior of pearl millet × napier grass interspecific hybrids. *Agronomy Journal* 72: 358-360.

Kalu, B. A. & G. W. Fick, 1981. Quantifying morphological development of alfalfa for studies of herbage quality. *Crop Science* 21: 267-271.

Muldoon, J. K. & C. J. Pearson, 1977. Hybrid pennisetum in a warm temperate climate: Re-growth and standover forage production. *Australian Journal of Experimental Agriculture and Animal Husbandry* 17: 277-282.

Ong, C. K., 1978. The physiology of tiller death in grasses. 1. The influence of tiller age, size and position. *Journal of the British Grassland Society* 33: 197-203.

Pritchard, G. I., L. P. Folkins & W. J. Pigden, 1963. The in vitro digestibility of whole grasses and their parts at progressive stages of maturity. *Canadian Journal of Plant Science* 43: 79-87.

Struik, P. C., 1983. The effects of short and long shading, applied during different stages of growth, on the development, productivity and quality of forage maize (*Zea mays* L.). *Netherlands Journal of Agricultural Science* 31: 102-124.

Tilley, J. M. A. & R. A. Terry, 1963. A two stage technique for the in vitro digestion of forage crops. *Journal of the British Grassland Society* 18: 104-111.

Warndorff, M., A. Dovrat & T. Kipnis, 1985. Quantifying tiller re-growth of hybrid pennisetum canopies. *Netherlands Journal of Agricultural Science* 33: 367-376.

Wilson, J. R., 1976. Variation of leaf characteristics with level of insertion on a grass tiller. 1. Development rate, chemical compostion and dry matter digestibility. *Australian Journal of Agricultural Research* 27:343-354.

Wilson, J. R. & D. J. Minson, 1980. Prospects for improving the digestibility and intake of tropical grasses. *Tropical Grasslands* 14: 253-259.

Wilson, J. R. & C. C. Wong, 1982. Effects of shade on some factors influencing nutritive quality of green panic and siratro pastures. *Australian Journal of Agricultural Research* 33: 937-949.
Woledge, J., 1978. The effect of shading during vegetative and reproductive growth on the photosynthetic capacity of leaves in a grass sward. *Annals of Botany* 42: 1085-1089.