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Pennisetum Americanum X P. Purpureum:
A Potential Forage Crop for Maximum Production
of Digestible Nutrients Under Subtropical Conditions

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Tal Kipnis and Amos Dovrat

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ABSTRACT

Highly productive tropical pearl millet x napiergrass interspecific hybrids have been bred at Tifton GA, USA. The aim of this project was to study the yield potential and quality of the hybrids under subtropical Mediterranean conditions prevailing in Israel. Thermal response of the plants was studied in the phytotron and the results make it possible to evaluate the thermal adaptation of the hybrids to various geographical regions. Sensitivity to low temperature was found to be a major limiting factor in achieving high annual yields. The effect of temperature on growth, development and digestibility of different plant parts was also studied, and parameters related to the canopy structure and regrowth in the field were verified with a descriptive simulation model.

Late maturing, day length sensitive lines of cytoplasmic male sterile pearl millet bred at Tifton can extend the period of vegetative growth into the autumn by approximately 40 days. Interspecific hybrids between these lines and napiergrass are expected to produce a high quality forage plant with a wider range of seasonal adaptation to regions with a subtropical and Mediterranean type climate.

The wide distribution and use of these hybrids will depend on efficient propagation procedure. The photoperiodic and temperature conditions in the Southern Arava region of Israel were shown to be suitable for successful hybrid seed production. Seeds were produced in late autumn and also in the spring by manipulating the time of flowering of the parental lines to occur simultaneously. Commercial hybrid seed production is being contemplated. In addition, a new method, using non-rooted aerial tillers, was developed for the vegetative propagation of the grass.

OBJECTIVES OF THE RESEARCH

1. To study yield components and digestibility of the interspecific hybrids as functions of temperature, defoliation and soil moisture.
2. To determine the relative importance of the above for:
 - (a) The definition of selection and breeding criteria, and (b) the design of management systems which will ensure maximum digestible dry matter yields.
3. To develop a late maturing pearl millet female parent, and to search for genotypes with wide seasonal adaptation.
4. To study the possibility of hybrid seeds producing in Israel.

PART I. INTRODUCTION

HYBRID PENNISETUM AS A FODDER FOR CATTLE IN TROPICAL AND SUBTROPICAL ENVIRONMENTS.

Origin

In the following description of pearl millet and elephant grass, we have not distinguished between different cultivars of these species. Both parents of the hybrid are tall, tufted grasses, which originated in tropical Africa.

Pearl millet (*Pennisetum americanum*) is an annual bunch grass, cultivated as a cereal grain in the drier parts of tropical Africa, India and Pakistan, and grown as a fodder in the USA. It has a reputation for being resistant to drought (3, 7, 28)

Pearl millet is phenotypically very variable, but generally produces culms of 2-3 metres, occasionally up to 5 m in height (7, 11, 14, 88). The stem solid (not hollow), when mature ranges from 8.5 to 19 mm in diameter at the base (12), bears leaves of 20-100 cm long and 5-50 mm wide (7) which are covered densely with hairs on both surfaces (51). It is a facultative short-day plant (4, 7), i.e. capable of flowering under long days (h. photoperiod), but earlier under short days.

Elephant grass (*Pennisetum purpureum*) is a robust perennial forage species with coarse and upright stems (up to 30 mm in diameter),

reaching a height of 3 to 4.5 metres (7 , 11, 34 , 87 , 88). The coarse leaves are 30-120 cm long and 10 to 50 mm wide, glabrous or hairy, especially towards the base, with a prominent midrib on the lower side (7 , 12, 51, 65 , 87). It spreads by short rhizomes to give stools up to 1 metre across (7 , 34 , 88). This grass tillers freely and often 50 or more tillers are produced from a single plant, which is much more than pearl millet (34, 51).

Elephant grass is valued for its high herbage yields, competitive vigour and persistence, but the foliage is highly susceptible to frost damage although the underground parts are not damaged seriously (7 , 28, 34).

Hybridisation between pearl millet and elephant grass probably occurs naturally since both species cross pollinate (60). In 1941 Burton (11) hybridized elephant grass with pearl millet, using elephant grass as the female parent. Later, hybrids have been produced in other countries as well, first in India (49), using pearl millet as the female parent. This latter approach has become the practice nowadays. In many tropical and sub-tropical areas, experiments with hybrid pennisetum have been carried out. As yet, however, the hybrid has not been commercially utilized.

Breeding aspects

Although observations showed that elephant grass reproduces sexually (38) and thus can be used as the female parent (22), the usual procedure is to use pearl millet as the female parent. Pollination is easily carried out by hand (71).

The choice of the proper parental combination is important. Some combinations produce seedling-lethal hybrids, others produce hybrids with varying yield potential (39). Especially in India and the USA extensive research has been carried out in order to develop cultivars of the hybrid with improved yielding ability and forage quality. Up to now, only a few cultivars have been released from these breeding programmes and thus there still is considerable scope for improvement.

In 1962 Tift 23 A, a cytoplasmic male-sterile pearl millet was officially released by the US. Dep. of Agriculture (13) to eliminate the need to enclose the flower-heads after pollination and distinguish hybrid from inbred seedlings.

In 1966 a method for commercial seed production of hybrid pennisetum was suggested in which the cytoplasmic male sterile pearl millet is sown annually between established rows of elephant grass and seed harvested from these rows. The perennial elephant grass would make it unnecessary to re-establish it each year, thereby reducing seed-production costs (71). For this method and for all other methods for seed-production, it has to be realized that it is restricted to areas which have long frost-free periods. It requires short days for flower initiation in the male parent and although pearl millet is only a facultative short-day species; to achieve synchronized flowering, a short-day photoperiod-sensitive pearl millet parent must be used.

Hybrids between pearl millet and elephant grass can be obtained and established from seed (39), but the F_1 progeny is sterile (1, 11, 38, 39, 49, 51, 77). The sterility is due to meiotic irregularities including chromatin bridges and laggards (i.e. chromosomes which show retarded movement) which lead to the formation of abnormal tetrads; pollen grains are therefore genetically and morphologically abnormal (60).

Morphological and physiological aspects

Morphologically the hybrid resembles elephant grass more closely than pearl millet, although it possesses some of the leafiness of pearl millet. Specific morphological features are either intermediate between the parents or approach those of elephant grass. Morphological variation occurs among hybrids from different parents and in different environments (60). Hybrid pennisetum is supposed to combine the high forage potential of elephant grass and the forage quality of pearl millet (1).

Hybrid pennisetum is an erect bunchgrass which grows to a height of 4-5 m. The culms are 1.4-2.4 cm in diameter. The soft pubescent and juicy leaves are maximum 85-110 cm in length. The hybrid produces 30-50 tillers and at maturity secondary branches arise from axillary buds along the stem. The main tiller produces 20-30 leaves. Most genotypes are non-rhizomatous and rapidly develop a shallow, fibrous root system (60).

Hybrid pennisetum probably has a NADP-malic enzyme type C₄-system (70) (i.e. the leaf mesophyll cells in which CO₂ is fixed by the C₄-dicarboxylic acid cycle export malate to the bundle sheath in which CO₂ is released by NADP-malic enzyme and refixed in the reductive pentose phosphate pathway).

The rates of photosynthesis of sunlit expanded leaves ranged from 80 ng CO₂ cm⁻²s⁻¹ in leaves that were grown at 33/28 °C to 20 ng CO₂ cm⁻²s⁻¹ at 18/13 °C. At the higher temperature regime, the rates differed according to leaf position in the order uppermost > middle > lowest leaves, whereas at 18/13 °C the rates of the uppermost (i.e. sunlit) leaves were similar to those of leaves in the middle of the canopy (68). The rate of photosynthesis is depressed at temperatures below 24 °C, an observation in agreement with that of Muldoon and Pearson who found a plateau in net assimilation rate (NAR) around this temperature (58).

The photosynthate is principally fixed as starch in the mesophyll cells, where it may be stored or exported (70). Although starch accumulates at lower temperatures (70), Pearson and Derrick did not detect a correlation between photosynthate retention and photosynthetic rates, which indicates that over a wide range of temperatures, starch concentration in the leaf does not affect the rate of photosynthesis (68).

Muldoon and Pearson (58) found that the maximum rate of tillering in hybrid pennisetum, growing in pots, followed a parabolic temperature response curve, e.g. in summer (photoperiod longer than 14 h) the maximum rates were 0.64, 0.39, 0.38 and 0.71 tillers per day for 18/13, 21/16, 27/22 and 33/28 °C resp. Tiller numbers, when counted at the end of primary growth, decreased with increasing temperature (up to 27/22 °C), even though the number of leaves per main tiller, and hence the possible sites for tiller production were similar.

The hybrid has the characteristic of producing lateral tillers from the leaf axils at the base of the main stem as soon as six leaves have emerged, irrespective of time from emergence, at any temperature (66).

The rate of leaf expansion, which increased up to 33/28 °C, is more important at temperatures above 20-25 °C than net assimilation-rate, which responded positively to temperatures only up to approx. 27/22 °C. The more rapid expansion of the total leaf area of plants at higher temperatures is associated with higher rates of leaf appearance (24, 44, 66, 89), faster expansion of individual leaves (44, 57, 58) and higher leaf area per unit weight (58). The area of individual leaves increases almost linearly with leaf number on the main tiller, until a maximum area is attained in the third leaf unfurled from the apex (66). Mean individual leaf area is greater at higher levels of insertion on the tiller and consequently, mean individual leaf area increased throughout primary growth (58).

This is in agreement with the finding that in grasses the rate of leaf and tiller production increases with temperature up to an optimum. Consequently, during initial growth, the total number of leaves and the total number of tillers increase exponentially (88). However, it must be kept in mind that temperature effects growth differently; e.g. at 24/19 °C the rate of production of new leaves on the main tiller is slower, but more tillering occurs so that the total number of new leaves is similar to that at 33/28 °C (66). This indicates that high tillering capacity is advantageous under both high and low temperatures; at high temperatures because leaf expansion dominates tiller initiation and at low temperatures because the growth rate of the whole plant is low.

In hybrid pennisetum as well as in other tropical bunch grasses, the increase in the growth rate of the whole shoot as influenced by increase in temperature is controlled by the growth of the individual tiller, rather than a change in the rate of tillering (44, 58). Therefore, a cultivar with a large number of small tillers is preferable to a plant with a few but heavy tillers; the former can be cut at more frequent intervals since it possesses plenty of sites for regrowth, and maximum crop growth rate would be reached earlier than in the latter.

After defoliation the number of tillers is initially high, because of the simultaneous regrowth of tillers from the stubble (56), perhaps partly due to a reduction in basal shading (79, 92). When potgrown plants were cut several times, the number of tillers increased throughout each regrowth period, except at temperatures above 21/16 °C, where a ceiling was attained two weeks after cutting. In this experiment, the number of tillers at the end of each regrowth period was 2-3 times greater than at the end of the preceding growth period. This multiplication of tillers in regrowth together with a initially higher rate of leaf production/tiller in regrowth, accounted for the increased rate of leaf production per plant in regrowth compared to primary growth (58).

The response of increase in dry weight with temperature was linear in regrowth too although in some cases the slope of the response curve tended to decrease after 27/22 °C (58, 59).

The fate of the apical meristem following defoliation is an important morphological factor (19, 59). The undamaged apical meristem of defoliated, non-elongated stems continues to produce new leaves after defoliation. But if meristem is removed or damaged by cutting in the elongated stems, leaf production depends upon new tillers arising from basal adventitious buds and axillary buds along the stem (59). The cutting of stem apices stimulates tillering by removing the major source of auxin which inhibits lateral bud development; inactive buds are then free to develop (92). This means that regrowth after defoliation arises from existing active meristematic tissues (usually fast) or from previous inactive axillary buds (slow); residual active meristematic tissues, including those of an immature inflorescence, are obliged to continue growth. Consequently, there is great variation in morphology and speed of leaf development, depending on growth stage (43).

Muldoon and Pearson found that changes in stem weight after defoliation were entrained with new growth: stem weight increased slightly in decapitated plants where new growth was largely delayed until after the development of adventitious buds and in hybrid at low temperature where new growth was slow, whereas stem weight decreased in intact plants having rapid new growth at 30/25 °C and 24/19 °C (59).

The initial rate of regrowth after cutting is, in addition to temperature, influenced by the fate of the apical meristem and presumably the level of carbohydrate reserves in stubble and roots at defoliation (59). It is generally assumed that the carbohydrate reserves needed for regrowth are transferred from the roots and stubble to the meristematic regions (37, 88), but Muldoon and Pearson did not detect a carbohydrate reserves transfer from the roots in hybrid pennisetum (59). These authors characterise regrowth after cutting as follows:

1. An initial decrease in dry weight of the regrowing stems associated with the translocation of their carbohydrate reserves to tissues closest to the site of new growth.

2. Translocation of more carbohydrate reserves into new growth, relative to that which was lost from the plant;
3. Limited mobilisation of reserve substances (proteins and polysaccharides) from old stem and leaf sheath.

The observed decrease in root weight following defoliation is presumably due to respiration (59) and/or death of roots from tillers not capable of regrowth after cutting.

A knowledge of the kinds and trends of energy-providing carbohydrates in the stem bases is important to cutting and grazing management studies, since the status of the carbohydrate reserve will indicate the periods of storage and utilization and the potential of hybrid pennisetum to regrow following defoliation.

In a review article on light and temperature requirements for the regrowth of grasses (20), Cooper and Tainton concluded that tropical species often fail to grow below 15 °C. Experiments which estimated the critical day temperatures at which growth would cease were generally below 12.5 °C and critical night temperatures below 10 °C, support that general finding (44). In hybrid pennisetum too, productivity is limited by sub-optimum temperatures (56 , 57 , 67).

The seedlings of hybrid pennisetum are unable to adopt to a decrease in temperature to 15/10 °C shortly after emergency (until one week after sowing they were kept at 24/19 °C), which suggests that the hybrid is relatively sensitive to thermal shock at about the time it enters a positive carbon balance (57). Cool temperature depression of dry weight accumulation is due not only to lower rates of net photosynthesis, but also to slower germination, slower and at 15/10 °C incomplete utilization of seed reserves, lower meristematic activity and top/root ratio (i.e. the distribution of carbohydrate between top and root), and probably lower rates of carbohydrate translocation (66).

The relatively better adaptation of hybrid pennisetum to low temperatures compared to pearl millet, is related to meristematic activity, leaf composition and photosynthate retention in source leaves (67 , 68 , 70).

No correlation was found between photosynthetic rates and growth rate in hybrid pennisetum, thus thermal adaption seems more closely related to utilization of photosynthate than to gross production (68). According to Pearson et al (70) the tolerance of hybrid pennisetum to low temperatures seemed not related to either accumulation of starch or direct physical damage to chloroplast or a mass-action negative feed back on photosynthesis.

Generally low temperature stimulates the formation of new tillers in tropical grasses (24, 25) and stem growth is more severely inhibited by low temperatures than leaf growth (44).

At a given chronological age hybrid pennisetum increases linearly in dry weight with temperature up to 33/28 °C; the optimum temperature for dry matter accumulation appears to be 30°C or higher (58, 66). In hybrid pennisetum as in other tropical grasses the leaf appearance rate/tiller is stimulated by high temperatures (24, 66). Although the rate of tillering increases with temperature, the tillering period is shortened probably because of an increased rate of stem elongation (58). High temperature promotes stem elongation which results in rapid ageing and also in a lower leaf/stem ratio. Thus tillers of the same chronological age will be physiological "older" and will bear heavier, less digestible stems than tillers growing in low temperatures (N application has the same effect) (15, 90).

Although there seemed to be a general association between rapid seedling establishment meristematic activity, flowering and rate of dry weight accumulation at different temperatures, Pearson (66) did not find a simple correlation between production, and expansion of leaves and rate of whole plant dry weight accumulation. This means that optimum temperatures must be specified in terms of a particular plant parameter.

As can be judged from the preceeding part of this chapter, already some progress has been made (especially in Australia) in investigating the physiological effects of temperature on hybrid pennisetum. On the photoperiodic response less information is available. It seems that this response varies greatly between cultivars; the most agronomically useful cultivars require short days for flowering (60).

Some cultivars have a photoperiod-insentive juvenile phase and after cutting do not flower until the photoperiod has decreased to 13 h. (56, 69). Under tropical conditions, some hybrids continue to flower throughout the year (18, 60).

Agronomic aspects

Hybrid pennisetum is easily propagated by stem cuttings or root stocks (48 , 67). The stem cuttings should preferably be taken from the lower two-third of the stem and taken from three-month-old rather than from six- or twelve-month-old stems. It was also found that stems with two buds cut and planted in a vertical position so that one bud remained above the soil (this being the one that sprouts), gave significantly higher germination than stems with two buds laid horizontally in furrows (46 , 65). In the sub-tropics, spring planting is supposed to be best (60 , 65).

In the humid sub-tropical climate of New South Wales, Australia (Ca-climate), Pearson and Anthony (67) planted single-stemmed cuttings of hybrid pennisetum at a depth of 7.5 cm with stems protruding above the ground and spray irrigated immediately after planting. This resulted in 99% plant establishment.

Planting densities vary, although a row spacing of 60 cm is common. The space between the plants within the row is mostly the same as the inter-row spacing or less (6 , 18, 65). Under frequent cutting stubble diameter reaches a maximum of 40 cm, so a 50 cm spacing gives almost complete ground cover (60). With tropical grasses in general, in humid tropics or under irrigation, close spacing gives the highest yields, whereas in the more arid areas a wider spacing is preferable to reduce plant competition for soil moisture and to allow development of the rootsystem under less favourable conditions (55).

Pearson and Anthony in humid sub-tropical Australia, assessed the productivity of hybrid pennisetum at different planting densities and found that a density of four or nine hybrids per m^2 produced twice the dry matter yield as compared to a density of one plant per m^2 (67).

Hardly any research is done to ascertain the optimum sowing conditions of hybrid pennisetum. This is probably due to the fact that

seed is not yet available in commercial quantities. Pearson et al sowed the hybrid during mid-summer in coastal New South Wales, Australia. They used 12 kg of seed per ha and sowed it in 10 cm rows; 50% emergence occurred after three days (69). Regarding the forage production of hybrid pennisetum under field conditions, no reliable data seem to be available from which maximum possible yields can be estimated. In various trials the hybrid outyielded other tropical grasses, including its parents, but usually a considerable range in yield is quoted. Muldoon and Pearson point out, presumably this range stems from variations in climate and cultural conditions, but inadequate reporting of these conditions makes it almost impossible to relate one study to another (60).

However, the overall picture is that the hybrid seems capable of yielding up to 250-300 t of green material per ha (23, 52, 65), although yields up to 400 t/ha or even more have been recorded (7, 60, 63). These yields were recorded under tropical conditions, mostly in India. Much less is known about the production under sub-tropical circumstances, but as a rather rough indication of the hybrid potential in these environments, one finds that it amounts to about half of the yields obtained under tropical conditions. Yields of approximately 100 tons of green material per ha have been obtained in South-Africa (28) and dry matter productions of 17-18 t/ha in Australia and 22 t/ha in the USA (39) are reported.

Hybrid pennisetum has the capacity to maintain production at a similar level for at least three years (56). Under sub-tropical conditions the production is markedly seasonal with a maximum production during summer. When temperatures fall below 22/12 °C there is hardly any or no growth at all (57, 67). Under these conditions it is an advantage to have a cultivar with a long vegetative period with the ability to produce forage in late summer and autumn until frost; thereby providing quality forage during a period of the year when most tropical grasses have declined in quality and yield (39, 69).

In tropical environments the rainfall incidence is the seasonal factor which has most influence on plant growth (64). The growth rate of hybrid pennisetum in Bihar, India (tropical wet and dry climate),

during the dry season is about one-tenth of that during the wet summer (79).

Under sub-tropical conditions there is also a difference between cultivars regarding wintergrowth. From field trials in North-India planted in August, cultivar NB 21 could give 3-4 cuttings up to January, against only one cutting for cultivar Pusa Giant Napier, which remained dormant thereafter (30, 52).

Therefore, rather than decide on fixed intervals between cuttings, in order to obtain a high production of hybrid pennisetum of good quality, one should adjust cutting intervals according to the season. The production of the hybrid increases with increase in the amount of fertilizer applied (8, 10, 17, 33, 57, 62, 83). The yield response to fertilizer N is linear, when moisture, temperature and radiation are all favourable. It seems that under tropical conditions this response is linear up to 1200 kg N/ha (33), while under sub-tropical conditions probably only up to 500 kg N/ha (8, 57). However, in sub-tropical environments it should be kept in mind that high N-fertilization endangers survival of hybrid pennisetum during winter, because of reduced cold resistance (57).

Split applications of N are superior to one application (50, 54, 65). It is also recommended that the fertilizer is applied when the rootsystem of the hybrid is well developed (62). During winter no fertilizer should be applied, since it not only affects the winter survival of hybrid pennisetum negatively, but it also appears that in that case few tillers are produced in spring and that this setback remains throughout the growing season (57, 65).

It is difficult to say anything specific about the response of the hybrids to fertilizers other than N, because little research has been carried out on this topic. In a trial lasting for 600 days in Gujarat, India, application of 120 kg N + 60 kg P_2O_5 + 60 kg K_2O /ha or N alone, gave total fresh yields of 2.27 and 2.04 t/ha respectively (74). These are extremely low yields, so probably anything else was limiting the growth. According to Muldoon and Pearson a yield of 20 t dm/ha, removes 100 kg each of P, Mg and Ca, together with 500 kg K. They therefore consider an annual rate of 100-200 kg P/ha adequate (60).

Forage yields can be greatly increased through cutting practices that maintain growth rates as near the maximum as possible. Therefore, cutting must be timed to coincide with the moment that the crop growth rate starts to decrease. Considerable efforts have been made in the investigation of the yield response of hybrid pennisetum to different cutting intervals and cutting heights in order to assess the optimum cutting schedule. Due to favourable conditions in the tropics, hybrid pennisetum can be harvested throughout the year with a cutting interval of about one month (11, 20, 63). Under sub-tropical conditions the cutting frequency is restricted mostly to 4-5 times per season (47, 57, 67).

Generally a cutting interval of 50 or 60 days has proven to give the highest yields (31, 61, 63, 84, 85), although Pritchard recorded greatest yields from a 12-weekly cutting regime and lowest yields from an 8-weekly frequency (72). In the sub-tropical environments of Australia a 6-weekly cutting interval throughout the summer is recommended (67).

As stated the location of the apical meristem affects the capability of tillers to regrow after cutting and hence the decision on the desirable cutting height. It is regarded desirable to leave a stubble height of at least 10-15 cm from the ground level so as to avoid slower regrowth from tillers cut below the apical meristem (56, 57, 65). Since grazing animals will remove more of the succulent plants parts containing the buds, regardless of the height of these terminal buds above the ground, grazing might be of greater damage than cutting (27). In trials with Pusa Giant, higher fresh fodder yields were obtained by cutting to a height of 30 and 45 cm (124 t/ha) than by cutting at 15 cm (112 t/ha), (84).

Mostly the cutting height is 15-20 cm (2, 18, 65, 67). Under sub-tropical conditions the winter survival of the hybrid is lessened by cutting it too low; e.g. in Australia the defoliation should not be below 20 cm in autumn (57).

It is difficult to draw conclusions from the scanty literature available, since very less field trials have been carried out. But to cite Muldoon and Pearson, "it appears that the hybrid, which has a strong regrowth capacity, is able to compensate for differences in cutting height and cutting schedule." (60).

In this chapter the emphasis has been on the yield response of hybrid pennisetum to different management systems regarding green forage and dm production. But it is well-known that factors as fertilizer, cutting interval and cutting height have considerable influence on the quality of the forage as well. In the next chapter we shall further elaborate this aspect.

Forage quality aspects

In hybrid pennisetum as in grasses in general, forage quality deteriorates with age, both in leaves and in stems. This means that the older, lower leaves and internodes deteriorate more than the top leaves and internodes. This process (i.e. ageing) proceeds faster at high temperatures than at low temperatures. Besides this, high temperature not only enhances the content of CF and cell wall constituents of a plant, but also stimulates lignification, thereby speeding up the deterioration of the forage quality (21, 22, 24, 90, 97).

In hybrid pennisetum the stems contain more lignin than the leaves at all stages of maturity (6, 76, 77). Lignin markedly depresses the digestibility of forage in the rumen, possibly by acting as a physical barrier between the enzymes and substrates. Therefore, the degree of deposition of lignin provides a rough index of the digestibility of a forage at a particular stage of growth (6, 24, 26, 80). Given the fact that the leaves contain more CF, etherextract, minerals than the stem, which is richer in CF and water soluble carbohydrates (76, 77), an important factor in determining the forage quality of hybrid pennisetum is the relative leafiness at the time it is used as a fodder (16). The continuous stem elongation is therefore bound to have its consequences for the ratio of leaf to stem and for the digestibility of the hybrid.

Consequently it is necessary to harvest hybrid pennisetum at a proper stage of growth to prevent it becoming woody (45). Patel et al in a tropical wet and dry environment found that the fodder obtained by harvesting at a 60-day cutting interval was fibrous and low in protein and etherextract, and would therefore be of inferior quality. More nutrients were obtained when the fodder was harvested at 50-day cutting intervals (63).

In Australia Muldoon and Pearson managed to maintain the forage quality at an adequate level (8.75% CF and 62% OM digestibility) in mid-Summer (humid sub-tropical area) with a 6-7 week cutting schedule (56)

In Thailand, Vilaipol found that the OM remained constant at a cutting frequency of 30, 45 or 60 days, but that a longer cutting interval decreased the contents of etherextract, CP and ash. He also found a decrease in the CF-content with a decrease in cutting frequency (85). This latter finding is in contrast with the fact that the CF-contents rise throughout the growth-period and with the observations of Patel et al who found an increase in CF-content with long cutting intervals (41, 63, 85).

Since N fertilization decreased the CF-content of the hybrid (83), it had a positive effect on the forage quality. At the same time the nutrient yield of hybrid pennisetum was always higher with NPK fertilization than with N alone (74).

Throughout the growth period the leaves contain higher total and protein N than the stem, whereby the stem N-content was generally 0.8-0.9% below that of leaves (56, 57, 76, 77). The total and true protein N-content decreased as the hybrid matured, but more in stems than in leaves (6, 56, 77, 78, 82). This decline in the concentration of N in the stem could either be due to the reduced supply of aminoacids from the leaves to the stem for synthesis of proteins or it might be a reflection of higher rates of synthesis of non-protein components in the stem (6).

Gore et al found that the N-content (as % of dm) did not differ between fertilizer treatments and frequency of cutting, and varied within the range of 2.4-3.0. But the response of hybrid pennisetum to NPK fertilizer or farm yard manure in terms of protein yield in kg/ha was highly significant, although not very consistent, since in one year yields were greater with 5 than with 8 cuttings whereas one year later 8 harvest yielded more than 5 (33). This example makes it clear that there is an inverse relation between herbage yield and CF-content. Therefore the choice of cutting dates always involves a compromise between yield and quality. Goonewardene and Appadurai who conducted an experiment with hybrid pennisetum in the wet zone of Ceylon, found that the point of intersection occurred at the 35th day of growth at which time the CF-content was about 15% (31).

Generally in grasses and also in the hybrid the CP-content decreases with a lengthening cutting interval (26, 41, 63, 84, 85, 86, 93), probably a normal result of maturity. Vilaipol found that the contents of N were highest when cutting was done at 45-day intervals (85), whereas according to Tomer et al CP yields were highest when cut at 50-day intervals (tropical restricted rainfall environment) (84).

The increase in the CP-content of hybrid pennisetum with an increase in cutting frequency, might be due to the stimulation of leaf production from basal buds by removing the apex (60). The CP-content of the hybrid responded positively to increasing rates of N-fertilizer (8, 57, 83). The concentration of water soluble carbohydrates of hybrid pennisetum increased with the development of the plant. It is much higher in stems than in leaves and this difference widened as the plant matured. Part of the water soluble carbohydrates synthesised in the leaves is translocated to the stem where it is stored both as reducing and non-reducing sugars (6, 77). This increase in the level of water soluble carbohydrates with advancing maturity of the forage is probably due to the fact that there was no seed-setting in the hybrid, which means no diversion towards the region of seed formation (5).

According to an experiment of Singh et al, the water soluble carbohydrate contents of the stem increased with age only up to 80 days after planting and then decreased (78).

An aspect of the chemical composition of hybrid pennisetum which has attracted considerable attention is its oxalate content. It is known that a high concentration of oxalic acid reduces the quality of green fodder as its regular feeding causes an imbalance of calcium in the animal body (6, 75). Oxalates, whether present as insoluble calcium salts or as soluble neutral acid salts or as free acid, originate from the oxidation of compounds such as sugars, amino-acids, alcohols and carboxylic acids (6). Soluble oxalates, interfere in the animal with the absorption of calcium, due to the formation of insoluble and unabsorbable calciumoxalate. Decalcification in the animal might be the result (82).

It is considered that a level of 4% and above of oxalate might be toxic. Besides this, a high oxalate content in feed can depress the butterfat content of milk (81).

Since the level of oxalate present in hybrid pennisetum generally does not exceed 3% (35, 52, 63, 78), it is probably too low to produce deleterious effects. Thereby, the concentration of oxalates gradually declines as the plant matures, both in leaves and in stem (6, 52, 77, 82). This decline may be due to the increased synthesis of water soluble carbohydrates, structural carbohydrates and lignin, leading to an apparent decline in the concentration (6).

Another point which is fortunate in this respect is the fact that the oxalic acid content seems amenable to genetic improvement. According to Sidhu and Gupta, protein, calcium and phosphorus have no relationship with oxalic acid content, while there is only weak association of oxalic acid content with green forage yield, tiller number, leafsize, leafwidth and plant height. This would mean that these traits can be improved with no or only minor effects on the oxalic acid content. There is however a positive association with stem thickness. Also a negative effect of leaf length on oxalic acid has been found. Development of a thin-stemmed hybrid (which is also more relished by cattle) with long leaves might therefore be advantageous (75).

Plant cells consist of cell walls and cellular contents; these cellular contents are almost completely digestible by ruminants, whereas the digestibility of cell-walls varies. Digestibility depends mainly on the lignin content of the cell-walls (24, 80). As stated earlier in this chapter, lignin encrustation of cellular structures restricts the ability of the digestive enzymes and rumen flora to attack the cellular contents and thereby reduces their digestibility.

Since the lignin content of the hybrid varies, it can be assumed that agronomic practices affect the digestibility of the grass.

No information is available on the influence of planting density on the forage quality of the hybrid. However, in an experiment with maize, Deinum found that plant density did not affect the digestibility of cell wall constituents or the percentage of cell wall constituents of leaves (21) (see also (40)).

In hybrid pennisetum the leaves have a higher in vitro dm digestibility than the whole plant, reflecting low digestibility values for the stem (62). This suggests that the digestibility of the hybrid may vary according to the cutting-regime, because of the differential rate of leaf production in regrowth. It must be remembered however, that although the dm digestibility may be increased by shortening the length of the cutting intervals, close or frequent clipping will generally reduce the total dm production of hybrid pennisetum.

Muldoon and Pearson in an experiment which they followed the regrowth of the hybrid throughout a 15-week growth period following defoliation, found that the digestibility of the stem-OM (including sheath) was higher than that of the leaves for the first ten weeks of regrowth (the stems at this stage consisted mainly of leaf sheath rather than true stems) (56). This higher digestibility is accounted for by the higher proportion of cell-contents in young stem material than in the leaf, but as the stem matures the cell-content fraction decreased rapidly and was replaced by cell wall material which became less digestible with increasing lignification (73). The digestibility of hybrid pennisetum decreases with advancing age, whereby leaf dm digestibility declines at a faster rate than for whole plants (56, 62). However, the digestibility is not significantly affected by age of stand (i.e. whether it is a first, second or third etc. year stand) (57).

Not much can be said about the general effect of N application on dm digestibility of hybrid pennisetum, since Muldoon and Pearson claim that digestibility is not significantly affected by the rate of N application (57), whereas Ogwanly and Mugerwa found that it increased dm digestibility (62). This latter finding however is in accordance with the finding mentioned earlier in this chapter that N fertilization

decreases the CF-content of hybrid pennisetum. In other tropical grasses however, it was found that the overall effect of N fertilization was to decrease the digestibility, except in young growth (42, 55,).

No clear conclusions regarding the forage quality of hybrid pennisetum can be drawn from the data presented in this chapter. In the following table (2) a compilation of data from various sources is presented.

Table 2. Composition of hybrid pennisetum forage

constituent	% dm		reference
	mean	range	
dm	21	14-30	9, 29, 33, 52, 53, 63, 76
CP	12	5-23	1, 2, 9, 29, 30, 31, 33, 35, 36, 39, 53, 56, 62, 63, 76, 88
CF	32	23-44	1, 29, 35, 53, 63, 76
ether extract	3	1-5	9, 29, 35, 63, 76
N-free extract	41	22-48	9, 29, 35, 63, 76
oxalic acid	2	1-3	35, 36, 52, 63, 77

Since one of the major nutritional factors limiting cattle production in the tropics and sub-tropics is the short supply of digestible material in forages, it is also necessary to consider the digestibility of the hybrid's forage in order to assess its quality.

In experiments carried out in the humid sub-tropical climate of the USA, Hanna and Monson found that in 4-week old hybrid pennisetum the in vitro dm digestibility ranged from 65-75%, while in 8-week old forage it ranged from 57-68% (39).

In a humid sub-tropical environment in Australia the OM-digestibility of the hybrid was 62% (6-7 week defoliation interval) (56), while an OM-digestibility of 67% was reported in a tropical monsoon climate (32).

Green hybrid pennisetum is relished by cattle and acceptability seems higher than of mature fodder (30). But even when hybrid pennisetum was cut at the dry season in Ghana (semi-arid climate), between 2.4 and 3 m tall and with a rather dry and stemmy appearance, bullocks and sheep ate all but the toughest stems readily (53).

The CP-digestibility of the hybrid is reported to be 67% in the cultivar NB 21 in the humid sub-tropical climate of India (30). Ogwany and Mugerwa (62) in the tropical wet and dry climate of Uganda found that the dm digestibility coefficients of the hybrid when well fertilized, ranged from 62 to 68% (4-weeks old regrowth).

Unfortunately no more data were found in the literature on the digestibility of hybrid pennisetum under different growing conditions. Also specific information on different cultivars is lacking. This makes it difficult to try and establish guidelines for management practices leading to an optimal balance between forage production and quality of the hybrid in tropical and sub-tropical environments.

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PART 2. THERMAL ADAPTATION STUDIES

INTRODUCTION

Since pearl millet and napiergrass originate in the tropics, they and their hybrids are well adapted to produce high annual yields under these conditions. When they are introduced to a less favorable climatic region particularly where low temperatures prevail during part of the year, their limited ability for thermal adaptation causes a significant reduction in potential productivity.

The short duration of the growing season in a Mediterranean climate is the main practical limit encountered in the introduction of tropical grasses.

Fig. 1 shows the actual and desirable seasonal growth curves in relation to daily maximum and minimum temperatures and to day length in most parts of Israel (32°N). Tropical grasses in Israel are productive during approximately 6 months. A better adapted grass is expected to give a further two months of productivity. The difference between the actual and the desirable dry matter production, shown for the spring (March), would be obtained from a grass adapted to grow at lower temperatures. The temperature late in the season (October) is high enough to ensure good productivity, and the decline in growth rate is related to day length shortening, which in short day plants, promotes reproductive rather than vegetative development.

In an attempt to attack the problem at both ends of the season we conducted research to analyze the growth response of hybrid *Pennisetum* to temperature, and, to develop a late maturing short day sensitive pearl millet and its hybrid with napiergrass. The latter will be discussed in part 7B of the report.

Fig. 1. Actual and desirable seasonal growth curves in relation to daily maximum and minimum temperatures and day length at Bet-Dagan, Israel.

A. ANALYSIS OF THE RESPONSE OF HYBRID PENNISETUM TO TEMPERATURE

ABSTRACT

Growth response to temperature was similar in three Pennisetum hybrids which differ in their morphology. Polynomial equations fitted to the data enabled the calculation of optimum and critical temperature for growth. The optimum temperature combination for maximum growth rate was 29.3/27.2°C day/night. Any deviation in diurnal temperature variation (DTV) greater than 5°C caused a sharp reduction in plant growth. Maximum plant growth with DTV of 13°C such as prevails in Israel, was 81% of that achieved with zero DTV. The possibility to predict the optimum and the critical temperatures for growth in different geographical regions can help in the evaluation of tropical grasses for successful introduction in subtropical regions.

Although hybrid pennisetum undergoes considerable acclimation to fluctuating temperatures which results in high growth rates during part of the year, better adaptation to low temperature is required to extend the growing season in subtropical regions.

Growth functions and changes in forage quality were calculated in relation to temperature regime. It is suggested that accumulation of degree days may serve as a reliable parameter for determining the optimum developmental stage for cutting of hybrid Pennisetum as long as photoperiodic conditions do not restrict vegetative development.

OBJECTIVES

1. To analyze the effect of temperature on growth and morphological attributes of different Pennisetum hybrids.
2. To define optimum and critical temperatures for growth of hybrid Pennisetum at different latitudes.
3. To evaluate the adaptability of hybrid Pennisetum to the Mediterranean climate which prevails in Israel.

MATERIALS AND METHODS

Plants of three hybrids 23AxN17, 23AxN20 and 23AxN23 (also designated as 17, 20 and 23) were raised from aerial tillers in 10L pots filled with 1:1 volcanic tuff vermiculite mixture (v/v). The plants were grown outdoors for 4 weeks and then transferred to the phytotron for another two weeks at $27/22 \pm 1^{\circ}\text{C}$ (day/night). At this time the plants were cut 10 cm above soil level.

A factorial experiment was carried out in which four day temperatures (td) of 17, 22, 27 and 32°C were combined with four night temperatures (tn) of 12, 17, 22 and 27°C .

Four phytotron rooms were each maintained at the following td/tn regimes: 17/12, 22/17, 27/22 and $32/27^{\circ}\text{C}$. Sixteen td/tn combinations were obtained by moving the plants between the four rooms twice a day, at 0800 and at 1600, i.e. at the beginning of td and tn periods, respectively.

The plants in the phytotron were grown under natural sunlight (approx. $26 \text{ MJ m}^{-2} \text{ day}^{-1}$) in July and August.

Natural daylength (approx. 14 h) was extended to 16 h with incandescent bulbs having very low photon flux density. Humidity was controlled during

the day, to provide a standard atmospheric saturation vapour deficit of 0.8 k Pa.

The plants were irrigated twice daily (0800, 1600 with "Nutricol 3" nutrient solution diluted to contain 210ppm N, 46ppm P and 184ppm K plus microelements.

The plants were maintained under the td/tn regimes for two growth cycles of 21 days each. They were cut at the end of each growth cycle and measurements were taken at the end of the second growth cycle. The experiment included two growth cycles so that the regrowth phase took place under the experimental td/tn combinations.

The following measurements were recorded from two replicates after cutting: Number of tillers, number of leaves, weight of leaves, weight of stems and leaf area.

The experimental variables are listed in table 1.

Table 1. Specification of variables

Variable	Definition	Unit
TOT-PLWT	total dry weight	g
DWT-L	dry weight of leaf blades	g
DWT-ST	dry weight of stems and leaf sheaths	g
PL-GR	plant growth rate	g day ⁻¹
L-GR	leaf growth rate	g day ⁻¹
ST-GR	stem growth rate	g day ⁻¹
No-L	number of leaves	
AV-LWT	average leaf weight	g leaf ⁻¹
LWT-R	leaf weight ratio	g g ⁻¹
L-AREA	leaf area	cm ²
AV-LSIZE	average leaf size	cm ² leaf ⁻¹
SPEC-LWT	specific leaf weight	g cm ⁻²
No-TILL	number of tillers	
AV-TILWT	average tiller weight	g tiller ⁻¹
AV-RGR	mean relative growth rate	g g ⁻¹ day ⁻¹
AV-NAR	mean net assimilation rate	mg cm ⁻² day ⁻¹
MDT	mean daily temperature	°C
DTV	diurnal temperature variation	°C
DD	degree day	°D
ACDD	accumulated degree days	°D

The growth variables were calculated according to Radford (1967).

RESULTS AND DISCUSSION

The analysis of variance for the main effects and their interactions are presented in Table 2. All the variables except two morphological attributes: No-L and No-Till were significantly effected by t_d and t_n . No-L was not effected by either day or night temperatures, and No-Till was effected only by the night temperature. Interactions of the first and the second order were significant for part of the variables, however they did not contribute to a better understanding of the response of the hybrids to temperature.

The hybrids were significantly different in all but two variables: DWT-L TOT-PLWT, and their growth rate form. Further analysis was conducted to establish the difference between the hybrids (Table 3). The main difference between the hybrids is related to tillering and its derivatives. The tillering potential of hybrid 17 was 18.4 and 35.1 percent higher than that of hybrids 23 and 20, respectively. Higher tillering potential is also reflected in No-L.

High tiller weight in hybrid 20 compensated for its low number of tillers. The high values for average leaf size and average leaf weight in hybrid 20 contributed to the high average tiller weight which finally resulted in non significant differences in plant growth rate between the hybrids. The response of growth and morphological attributes to temperature will be presented as means for the three hybrids.

The highest growth rate was achieved under a constant day and night temperature regime of 27°C . The response of the hybrids to day or night temperature relative to 27°C is illustrated in Fig. 2. Due to this way of presentation it is easy to distinguish between variables which are responsive and those which are not responsive to temperature. It is also

Table 2. Analysis of variance for the main effects and their interactions.

Variable ¹⁾	YB	Td	HYBxTd	Tn	HYBxTn	TdxTn	HYBxTdxTn
PL-GR		***		***		***	*
L-GR		***		***		**	*
ST-GR	***	***		***		***	**
No-L	***		*			***	
AV-LWT	***	***	***	***	***	**	
LWT-R	***	***		***	***	***	**
L-AREA		***		***		***	***
AV-LSIZE	***	***	***	***	***	***	
SPEC-LWT	*	*		*			
NO-TILL	***		**	***		**	*
AV-TILWT	***	***	***	***	***	***	***
AV-RGR	*	***	*	***		***	***
AV-NAR	***	***		***			*

* ** *** Significant at 0.05, 0.01 and 0.001 probability level respectively.

1) Variables are specified in Table 1.

Table 3. Main effect of temperature on various growth and morphological attributes in three pennisetum hybrids.

Variable ¹⁾		HYBRID		
		23A x N17	23A x N20	23A x N23
PL-GR	(g day ⁻¹)	3.88a ²⁾	3.10a	3.38a
L-GR	(g day ⁻¹)	2.11a	2.18a	2.06a
ST-GR	(g day ⁻¹)	0.96b	0.91b	1.31a
No-L		294 a	184 c	252 b
AV-LWT	(g leaf ⁻¹)	0.15c	0.27a	0.17b
LWT-R	(g g ⁻¹)	0.74a	0.74a	0.65b
L-AREA	(m ²)	1.24b	1.43a	1.30ab
AV-L SIZE	(cm ² leaf ⁻¹)	42.5 c	84.2 a	51.6 b
SPEC-LWT	(g cm ⁻²)	0.37a	0.33b	0.34ab
No-TILL		51.3 a	33.3 b	41.9 b
AV-TILWT	(g tiller ⁻¹)	1.32c	2.45a	1.82b
AV-RGR	(g g ⁻¹ day ⁻¹)	0.29b	0.30ab	0.31a
AV-NAR	(mg cm ⁻² day ⁻¹)	2.24a	2.04b	2.40a

1) Variables are specified in Table 1.

2) Hybrid means followed by the same letter are not significantly different (P = 0.05) according to the Duncan's New Multiple Range test.

Fig. 2. Response to day and night temperature of various plant attributes relative to their value at 27°C. (Parameters are specified in table 1).

day ----- night———

Relative response

Relative response

easy to identify variables which respond to day and night temperature in the same or in different fashions.

Variables like No-L, SPEC-LWT or LWT-R do not respond to change in either t_d or t_n . Leaf attributes like L-AREA, AV-LSIZE and AV-LWT responded similarly to day and night temperatures. Strong temperature responses were evident in the growth variables of the leaves, stems, tillers and the whole plant. The rise in day temperature above 27°C with any combination of night temperature reduced the growth rate of the leaves and the stems by 20 to 30%.

A weak response, not more than 20% relative to 27°C day or night temperatures was found in parameters like RGR or NAR. Number of tillers appears to be an exception to the rule. It was not affected by rising day temperature but was steeply reduced in response to rising night temperature.

Second-order polynomials were fitted to the data obtained from the 16 t_d/t_n combinations. The partial regression coefficients and coefficients of determination for the calculation of the experimental variables are presented in Table 4. The values for r^2 ranged between 0.233 and 0.947. 74% of the entries had r^2 values above 0.8, and only two regressions had r^2 values lower than 0.6. The growth variables (PL-GR, L-GR, ST-GR) had values higher than 0.8. Consequently these regressions can be used with some confidence to predict optimum or critical temperatures for growth.

The results show that the response to t_d/t_n combinations can be explained not only as functions of t_d , t_n or mean daily temperature (MDT), but that it is also in relation to the diurnal temperature variation (DTV). One of the purposes of this study was to clarify to what extent hybrid Pennisetum plants are able to produce high dry matter yields under

Table 4. Partial regression coefficients and coefficient of determination for the calculation of the experimental variables.

Variable ¹⁾	td	tn	td ²	tn ²	tdtn	intercept	r ²
PL-GR	910.11	513.65	-18.016	-12.401	5.47365	-15261	0.827
L-GR	501.45	322.92	-9.145	-6.573	0.89111	-8405	0.832
ST-GR	408.66	190.74	-8.871	-5.827	4.58254	-6855	0.808
No-L	21.02	11.83	-0.293	-0.116	-0.35053	-103	0.233
AV-LMT	0.03	0.02	-0.001	-0.000	0.00045	-1	0.938
LMT-R	-0.08	-0.07	0.001	0.001	-0.00002	2	0.947
L-AREA	2267.50	1405.66	-39.022	-24.302	8.34860	-39052	0.798
AV-LSIZE	7.56	2.10	-0.154	-0.047	0.13845	-116	0.929
SPEC-LMT	0.02	0.00	-0.000	-0.000	0.00015	0	0.440
No-TILL	3.13	-1.23	-0.027	0.064	-0.09600	26	0.736
AV-TILLMT	0.45	0.05	-0.011	-0.004	0.00984	-6	0.915
AV-RGR	0.02	0.02	-0.000	-0.000	-0.00007	0	0.889
AV-NAR	0.40	0.27	-0.008	-0.007	0.00086	-5	0.896

1) Variables are specified in Table 1.

Mediterranean as opposed to the equatorial temperature conditions. That was the rationale behind the experiments designed to elucidate the response of the growth variables to different diurnal temperature variation under the same mean daily temperature. The relatively good fit of the polynomial regressions allows an examination of the relationship between different DTV and the morphological or growth attributes at any MDT. Fig. 3 presents this form of analysis under mean daily temperatures of: 22, 27 and 32°C.

The highest PL-GR at MDT of 27 and 32°C is achieved under constant temperature regime i.e. when DTV = 0°C. At lower MDT the highest growth rate was achieved when t_d was 5°C higher than t_n . Any deviation in DTV greater than 5°C caused a sharp reduction in PL-GR. The variables related to the leaves (L-AREA, AV-LWT, AV-LSIZE), responded best at zero DTV as was found for the growth attributes, but the degree of response in the former was much more affected by MDT.

The leaf variables responded best to t_d of 32°C. A change in DTV from 0 to 10° caused a reduction in the rate of the response but to a lesser extent than the growth variables. Number of leaves was affected in a different manner. It seems that MDT of 22°C is more conducive to the production of new leaves than MDT of 27°C or 32°C. This effect is mediated by the low night temperatures (and therefore lower MDT) which favors tillering rather than the rate of leaf appearance on a single tiller which responds positively to high temperature. The difference between t_d and t_n has no effect on leaf production under favorable MTD conditions. However, under higher MDT, leaf production decreased as DTV increased. A mean daily temperature range of 22 to 27°C during the growing season is relevant to a location such as Bet Dagan in Israel. Within this temperature range, the reduction in the number of leaves per plant caused by a shift in DTV from 0 to 13° is estimated to be approximately 20%.

Fig. 3. Relationship between diurnal temperature variation (DTV) and various plant attributes for mean daily temperature (MDT) of 22, 27 and 32°C (Parameters are specified in table 1).

22 ———
27 - - - - -
32 - . - . -

NO-L

NO-TILL

AV-LWT

AV-TILLWT

L-AREA

SPEC-LWT

AV-LSIZE

AV-RGR

AV-NAR

Prediction of the optimal and the critical temperature

A response surface was fitted to the data for the calculation of optimal and critical temperatures relevant to the experimental variables. Two computer outputs concerning the variable PL-GR are presented in Figs. 4 and 5. Fig. 4 shows the response of the growth rate to t_d and t_n , whereas Fig. 5 shows that response as a function of daily degree days (DD) and DTV. The contour arrangement in these figures represents lines of equal growth rate for the levels of 30, 50, 70 and 90% of maximum growth rate. The outer line which was calculated by extrapolation, represents the critical temperature combination under which growth ceases. The optimum temperature combination at which maximum growth rate would be attained was 29.3 and 27.2 (t_d , t_n) and 14.4 DD and 2.2°C DTV, respectively. Threshold temperature for the calculation of degree days was 13.5°C.

The growth response to temperature is presented also as three dimensional response surfaces in Figs. 6 and 7.

These surfaces show that day and night temperatures do not act independently but interact in their effects on growth. Table 1 shows that such an interaction is significant for all variables except SPEC-LWT and AV-NAR. This means that the optimum day temperature required for achieving the maximum value for growth attributes, depends on the accompanying night temperature and vice versa.

Ivory and Whiteman (1978) calculated the optimal temperatures for growth in five tropical grasses. The optimal values that they report within and between species were very different. We shall therefore compare our results only with those Ivory and Whiteman report for Kikuyu grass, since it, at least, belongs to the same genus (Table 5).

Fig. 4. Optimum and critical temperatures and lines of equal growth rate (as percentage of the maximum) of hybrid pennisetum as related to day and night temperatures at different latitudes (3,5,7 and 9 representing 30,50,70 and 90% respectively).

Fig. 5. Response surface of growth rate of hybrid pennisetum as a function of degree day and diurnal temperature variation.

Fig. 6. Response surface of various plant attributes to day temperature (td) and night temperature (tn). (Parameters are specified in table 1).

Fig. 7. Response surface of various plant attributes to degree day (DD) and diurnal temperature variation (DTV).

AV RGR

AV RGR

AV NAR

AV NAR

Table 5. Optimum day and night temperatures for growth and morphological attributes of two pennisetum species

Variable ¹⁾	<u>P. americanum x P. purpureum</u>			<u>P. clandestinum</u> ²⁾		
	td(°C)	tn(°C)	DTV	td(°C)	tn(°C)	DTV
PL-GR	29.4	27.2	2.2	29.4	25.6	3.8
L-GR	28.7	26.5	2.2	29.8	26.3	3.5
ST-GR	30.3	28.3	2.0	29.2	26.1	3.1
No-L				23.8	27.7	-3.9
AV-LWT	36.3	38.6	-2.3			
L-AREA	32.7	34.5	-1.8	29.8	26.7	3.1
AV-LSIZE	*	*		34.1	25.7	8.4
SPEC-LWT	21.2	13.3	7.9	**	**	
No-TILL	17.7	22.8	-5.1	21.1	25.6	-4.5
AV-TILLWT	*	*		32.2	26.8	5.4
AV-RGR	27.8	23.5	4.3	28.3	25.8	2.5
AV-NAR	26.3	21.3	5.0	28.0	23.5	4.5

1) Variables are specified in Table 1.

2) From Ivory and whiteman (1978)

* Optimum temp. undefined but above 40°C

** " " " below 10°C

Table 5 shows the optimal temperatures and DTV at which maximum values are achieved for morphological and growth attributes in two Pennisetum species: P. americanum X P. purpureum (hybrid Pennisetum) and P. clandestinum (Kiku yu grass).

There are similarities as well as differences between the two species, showing that within the genus Pennisetum there is considerable variation in the response to temperature. There are differences in both optimal day and optimal night temperatures between the variables of each species. Furthermore, optimal t_d and t_n combinations are distributed over a very wide range of DTV. Maximum leaf area and leaf weight require high temperatures with negative DTV values of -1.8 and -2.3, i.e. $t_n > t_d$. Maximum leaf and stem growth is achieved under lower temperatures when t_d was 2°C above t_n . The small differences in optimal t_d/t_n for leaf and stem growth have morphological and physiological implications of practical importance due to their effect on stem/leaf ratio and therefore on productivity and nutritional quality. Again, tillering differs from the other experimental variables. The optimum temperature regime for tillering was found to be 17.7 (t_d) and 22.8°C (t_n).

In Fig. 4 the critical temperature combination for PL-GR under equatorial (DTV = 0°) and Mediterranean (DTV = 13°) conditions is indicated by the intersection between the zero growth contour and the two diagonal lines that represent the t_d/t_n regime in regions differing in their amplitude of DTV. The lower line marks constant t_d/t_n which might be expected at different altitudes in equatorial regions, the upper line marks the fluctuating temperature regime with a DTV of 13° that prevails during the growing season in Israel.

Under constant conditions (DTV = 0°), critical night temperature was 14.3°C. Under fluctuating conditions of DTV=13, growth ceases at 20.8/7.8°C td/tn. This would suggest that plants of hybrid Pennisetum are able to grow under cooler night temperatures provided that day temperatures are sufficiently high. The critical temperatures calculated for growth variables are presented in Table 6.

Table 6. Calculated critical tempratures for growth attributes (average of 3 hybrids).

a. Under DVT of 0 and 13.

Variable	DVT=0 (td=tn)	td	DVT=13 tn	MDT
PL-GR	14.3	20.8	7.8	12.1
L-GR	13.4	19.9	6.9	11.2
ST-GR	15.5	22.0	9.0	13.3
AV-RGR	5.1	11.7	-1.3	3.0
AV-NAR	10.3	16.7	3.7	8.0

b. The change in critical night temperature for PL-GR for 2° C increments in day temperature

td (°C)	Critical tn (°C)	DTV range (°C)
14.3	14.3	0
16.3	11.2	5.1
18.3	9.4	8.9
20.3	8.1	12.2
22.3	7.3	15.0
24.3	6.7	17.6
26.3	6.6	19.7

The quadratic equation yielding PL-GR=0 is:

$$15260.5 = 910td + 514tn - 18.016td^2 - 12.401tn^2 + 5.4737tdtn$$

in the range of td/tn=14.3/14.3°C to td/tn=26.3/6.6°C

corresponding to DVT 0 and DVT 19.7 respectively.

Acclimation vs. Adaptation

According to Kramer,⁽¹⁹⁸⁰⁾ adaptation refers to the heritable modifications in structures or functions that increase that the probability of an organism surviving and reproducing in a particular environment, or both. Acclimation refers to the nonheritable modification of characters caused by exposure of organisms to new climatic conditions, such as warmer, cooler, or drier weather.

Various responses to different DTV conditions in the range of 10 to 30°C MDT are shown in Fig. 8. The maximum PL-GR under DTV of 13° was 81% of that achieved at zero DTV. Optimum MDT for maximum PL-GR under zero and 13°C DTV was 28.4 and 25.°C td/tn respectively. Fig. 8 indicates that under contrasting DTV conditions, hybrid Pennisetum plants are able to achieve their maximal PL-GR at different MDT values. This means that the plants undergo considerable acclimation to fluctuating temperatures. This is a desirable trait since the seasonal (April-October) MDT at Bet Dagan is 23°C and the expected growth rate as shown in Fig. 8 is similar to the highest rate under DTV of 13°C. We suggest that attainment of this high growth rate is due to the acclimation ability of the plants. It is also shown that MDT which is critical at DTV 13 is only 2°C lower than the critical temperature under zero DTV. This suggests that due to acclimation to suboptimal growing conditions, the plants show a slightly better adaptation to low temperature. Unfortunately the 2°C difference in the critical temperatures at DTV 0 and 13 is too small to have agronomical significance at the beginning of the growing season when MDT is low. It is clear from the data presented in Fig. 8 that for the lower range of MDT, growth response is as strong under fluctuating temperatures as it is under constant td/tn conditions.

Fig. 8. Relationship between mean daily temperature and various plant attributes for DTU 0 and 13. (Parameters are specified in table 1).

DTU 0 ———
DTU 13 - - - - -

No-L

No-TILL

AV-LWT

AV-TILWT

L-AREA

SPEC-LWT

AV-LSIZE

LWT-R

AV-RGR

AV-NAR

Tillering potential is much higher under DTV of 13° than that under DTV of 0 (Fig. 8). However its maximum value is achieved at a very low MDT. In response to a rise in MDT, tillering decreased drastically as leaf growth increased. At MDT of 23°C, there was no difference in tillering potential between the two DTV combinations.

Another point of practical importance is related to the small difference (2°C) which was found in the critical MDT for leaf and stem growth. This is the reason why stem elongation in hybrid Pennisetum plants starts relatively early in the growing season.

Geographical adaptation

One of the purposes of this study was to evaluate the degree of adaptation of hybrid Pennisetum to geographical locations having suboptimal climatic conditions. In Fig. 9 the mean daily maximum and minimum temperatures from January to December for Bet Dagan and Eilat in Israel, have been superimposed on the lines of equal growth rate derived from the phytotron study. During part of the year, both locations have favorable conditions for the growth of hybrid Pennisetum. It appears that the temperature conditions in Eilat are more suitable for achieving high growth rates than the conditions at Bet Dagan.

The locations differ in length of growing seasons. At Bet Dagan, winter temperatures impose severe restrictions on the growth of tropical grasses. It can be seen that the earliest month in which 70% of maximum growth rate is reached at Bet Dagan is June, whereas at Eilat this occurs as early as April.

At Bet Dagan the range of temperatures prevailing during the April-October season limit growth from 30 to 80% of the potential growth rate. This is far below the values for Eilat for the same period.

Growing conditions in the phytotron are obviously different from those in the field. Therefore one should be careful in extrapolating the above findings to field conditions.

However, the results can serve as a guide for better understanding the limitation which a geographical location may impose on growth.

Fig. 9. Lines of equal growth rate for hybrid pennisetum as related to day and night temperatures and to mean maximum/minimum temperatures from January to December for Bet Dagan • and Eilat ○

The relative advantage of the Mediterranean region over the tropics with respect to productivity of tropical grasses is expressed in daily growth rate rather than in annual yield.

A mean crop growth rate of approximately $250 \text{ kg ha}^{-1}\text{day}^{-1}$ was calculated for hybrid 23AxN23 grown at Bet Dagan for 200 days under 'no stress' management and cut four times at intervals of approximately 50 days.

The high mean daily radiation which is required for high photosynthetic rates in C_4 grasses as well as mean daily temperatures of 23°C and 'no stress' management conditions, provide the means for attaining very high growth rates. The strong response of tropical grasses to temperature is a desirable character under conditions of small seasonal or daily temperature fluctuations. In Mediterranean conditions where the seasonal temperature fluctuation is large, strong temperature response is necessarily associated with a short growing season. Although acclimation results in high growth rates during part of the year, better adaptation to low temperature is required to extend the growing season in spring for the production of high annual yields.

In the field experiment mentioned above, the annual production of hybrid 23AxN23 was compared with the production of its male parent N23. The annual yield of the hybrid was better than that of its parent. However, it started to produce later in the season indicating narrower thermal adaptation as shown in Fig. 10.

There appears to be genetic variability for cold tolerance in the genus Pennisetum. This trait has not yet been incorporated into the hybrids, but could profitably be used in future breeding programs for the development of new genotypes that show a wider thermal adaptation than the hybrids presently available.

Fig. 10. Dry matter yields of napiergrass N23 and its F1 hybrid 23AXN23 in response to accumulated degree days (ACDD) over 200 days (threshold temperature for the calculation of ACDD = 12.2°C).

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**B. INFLUENCE OF TEMPERATURE REGIME ON DRY MATTER ACCUMULATION
AND DIGESTIBILITY IN PLANTS OF TWO PERNISETUM HYBRIDS**

OBJECTIVES

1. To study the effect of ambient temperature on the rate of development, dry matter accumulation and digestibility of different parts of the plant.
2. To calculate growth functions in relation to temperature, age, and canopy structure.

MATERIALS AND METHODS

Single plants of two interspecific hybrids 23A x N17 and 23A x N20 were established in 10l pots containing a 1:1 volcanic tuff vermiculite mixture. The plants were allowed to establish for 4 weeks outdoors in midsummer; they were then cut to a height of 7 cm above the soil surface and transferred to the phytotron where they were grown for 8 weeks under 16 h day length and 3 temperature combinations: 32/22, 27/17 and 22/12°C (day/night). The plants were irrigated every morning with "Nutricol 3" solution (as described earlier) and every afternoon with tap water.

Every week, starting from the first week after cutting, one plant of each hybrid and temperature treatment was selected at random for morphological analysis, dry weight distribution, (70°C oven dried) in vitro dry matter digestibility (IVDMD) using the Tilley and Terry procedure and

crude protein (CP) analyses (Kjeldahl-N x 6.25). The experimental variables are specified in Table 1.

Table 1. Specifications of variables.

Variable	Definition	Unit
TOT-PLWT	whole plant dry weight	g
DWT-L	dry weight of leaf blades	g
DWT-ST	dry weight of stems+leaf sheath	g
PDM-PL	percentage DM of whole plant	%
PDM-L	percentage DM of leaf blades	%
PDM-ST	percentage DM of stem+leaf sheath	%
DIG-TOT	dry matter digestibility of whole plant	%
DIG-L	dry matter digestibility of leaf blades	%
DIG-ST	dry matter digestibility of stems+leaf sheath	%
CP-TOT	crude protein of whole plant	%
CP-L	crude protein of leaf blades	%
CP-ST	crude protein of stem+leaf sheaths	%
No-L	number of leaves/plant	
No-TILL	number of tillers/plant	
SPER-L	weight ratio between stems and leaves	
EXPL-TIL	number of expanded leaves/tillers	
ACDD	accumulated degree days	

RESULTS AND DISCUSSION

Morphology

The temperature regime significantly affected the number of tillers per plant. The lower the temperature, the higher was the number of tillers. The lowest temperature regime also resulted in the highest total number of leaves but in the least number of expanded leaves/tiller and the lowest stem/leaf weight ratio (Table 2).

Tillering was better and there were many more leaves in hybrid 17 than in hybrid 20, however both the number of expanded leaves/tiller and the stem/leaf ratio were similar in the two hybrids.

Age was the sole factor influencing the number of fully expanded leaves. During the first 4 weeks of growth, a mean of 3.4 leaves/tiller reached full expansion. During the second 4 weeks of the experiment, the rate of leaf expansion decreased to 1.1 leaves per tiller, so that at day 56 an average of only 4.5 leaves per tiller were fully expanded. Tillering follows the same trend as leaf expansion due to enhancement of stem elongation between the 4th and the 8th week of growth.

Distribution of dry matter

Differences in dry matter percentage (PDM) between the leaves and the stems were greater than the differences due to temperature treatments, the hybrids or even between chronological ages (Table 3). The mean PDM of leaves was 15.6, and it was 6.1 units higher than that of the stems. Temperature had a slight effect on PDM in the leaves and stems, but had no effect on the canopy as a whole. Although PDM increased up to 22.0 and 16.2% in the leaves and the stems of 8 week-old grass, it should be noted

Table 2. The effect of temperature, hybrid and age on morphological attributes of hybrid pennisetum.

SOURCE	No-TILL ¹⁾	No-L	EXPL-TIL	SPER-L
<u>Temperature</u>				
32/22(°c)	15.7 b ²⁾	128.0 b	4.4 a	1.3 a
27/17(°c)	20.1 b	140.4 b	3.3 b	1.1 b
22/12(°c)	33.2 a	192.1 a	2.2 c	0.7 c
<u>Hybrid</u>				
23AxN17	26.8 a	176.9 a	3.3 a	1.0 a
23AxN20	19.1 b	130.1 b	3.3 a	1.0 a
<u>Age (weeks)</u>				
4	20.0 c	134.6 c	3.4 b	0.9 c
8	32.8 a	241.1 a	4.5 a	1.7 a

1) Variables are specified in Table 1.

2) Values in columns followed by the same letter are not significantly different (P = 0.05) according the Duncan's New Multiple Range test.

Table 3. The effect of temperature, hybrid and age on dry matter variables of hybrid pennisetum.

SOURCE	PDM-L ¹⁾	PDM-ST	PDM-PL	DWT-L	DWT-ST	TOT-PLWT
<u>Temperature</u>						
32/22(°C)	16.5a ²⁾	10.1a	12.3a	53.4a	90.9a	144.3a
27/17(°C)	15.5b	9.7a	11.8a	40.2b	60.5b	100.7b
22/12(°C)	14.8b	8.6b	11.7a	25.3c	19.9c	45.2c
<u>Hybrid</u>						
23AxN17	15.0b	8.6b	11.2b	38.0b	56.5a	94.5b
23AxN20	16.2a	10.3a	12.6a	41.9a	59.3a	101.2a
<u>Age (weeks)</u>						
4	15.2c	7.2e	10.6d	33.5e	33.3e	66.8e
8	22.0a	16.2a	18.0a	74.0a	141.8a	215.8a
<u>Plant part</u>						
Leaves			15.6			40.0
Stems			9.5			57.9

1. Variables are specified in Table 1.
2. Values in columns followed by the same letter are not significantly different (P =0.05) according to Duncan's New Multiple Range test.

that PDM values in the hybrids were low in comparison with other tropical grasses of the same age.

Leaf, stem and total dry weight were significantly influenced by temperature. A mean response of approximately 40 g dw/plant was measured as a result of a 5°C change in ambient temperature. The effect of temperature on dry matter accumulation was more pronounced in the stems than in the leaves. The average weight of leaf blades accumulated under the temperature regime of 22/12°C was 47% of that accumulated under 32/22°C. In contrast, under 22/12°C, mean stem weight reached only 22% of DWT-ST accumulated under 32/22°C. The sensitivity of stem growth to temperature which is expressed here as the stem/leaf weight ratio could be of significant practical importance regarding the distribution of dry matter in the different plant parts at different times of the year. The differences of total d.w between the hybrids was small but statistically significant.

The age effect was greater than that of either temperature or hybrid. DWT-L increased 2.2 fold and that of the stems 4.3 fold between the 4th and the 8th week of growth. Stem/leaf ratio of the mature grass was nearly twice as high as that of the young canopy, but there were no differences between the hybrids (Table 1).

Nutritional aspects

In general, the in vitro dry matter digestibility (IVDMD) measured in plants grown in the phytotron was very high in all treatments (Table 4). It was also higher than those determined in plants grown in field trials conducted under this program. The values obtained for crude protein were in the range of those in other experiments.

Table 4. The effect of temperature, hybrid and age on quality attributes of hybrid pennisetum.

SOURCE	DIG-L ¹⁾	DIG-ST	DIG-TOT	CP-L	CP-ST	CP-TOT
<u>Temperature</u>						
32/22(°c)	70.0c ²⁾	69.9c	69.4c	15.6c	10.7c	13.0c
27/17(°c)	72.8b	74.6b	73.3b	17.9b	12.8b	15.3b
22/12(°c)	76.7a	78.1a	77.1a	21.2a	17.6a	19.3a
<u>Hybrid</u>						
23AxN17	72.8b	73.5b	72.5b	18.5a	13.6a	15.7a
23AxN20	73.5a	75.0a	73.9a	18.0a	13.8a	15.9a
<u>Age (weeks)</u>						
4	72.5cd	77.4b	74.3cd	19.0d	14.8c	15.4c
8	72.4cd	66.8e	68.6f	12.2g	6.4e	8.6f
<u>Plant part</u>						
Leaves			72.9			18.3
Stems			74.1			13.7

1) Variables specified in Table 1.

2) Values in columns followed by the same letter are not significantly different (P = 0.05) according to Duncan's New Multiple Range test.

As expected, the digestibility of the two hybrids was better under the low growing temperature than under the higher ones. For both hybrids the mean IVDMD values for leaves and stems were very similar.

Although IVDMD was significantly higher in hybrid 20, it was only 0.7 and 1.5 % units higher than for hybrid 17 in leaves and stems respectively. Leaf (DIG-L) and stem (DIG-ST) digestibility of plants grown under 32/22°C were similar, whereas at the lower temperatures, stem digestibility exceeded that of the leaves. This can be explained by the relatively high number of immature stems developing on the plant under cooler growing conditions.

On a relative basis, the effect of temperature on CP was greater than its effect on IVDMD. As a mean for the whole growth period, CP content was higher at low temperatures than at high ones and in leaves than in stems. Total CP decreased with an average of 3% units for any 5°C reduction in temperature. CP content was similar in both hybrids, and showed a marked decrease with age.

Change in dry weight and nutritive value with plant age

A. Dry matter

Dry matter content of the leaf blades (PDM-L) increased almost linearly during the first four weeks of the experimental period. From that time, the further increase of PDM-L depended on the temperature (Fig. 1a). PDM-ST at the age of 4 weeks did not exceed 7%, and the further increase of PDM-ST with age was not affected by temperature (Fig. 1b).

The effect of temperature on the accumulation of dry matter during 8 weeks of growth is shown in Figs. 2a and 2b. The accumulation of dry matter follows linear and curvilinear patterns for leaves and stems respectively.

Fig. 1. Relationship between percentage dry matter of leaves (A) and of stems (B) and age as a function of temperature.

Fig. 2. Relationship between dry weight of leaves (A) and of stems (B) and age as a function of temperature.
 □ 32/22(°C) Δ 27/17(°C) + 22/12(°C)

At the end of the 8th week of growth, dry matter accumulation at 22/12°C in the stems was only 23% of that accumulated at 32/22°C, whereas in the leaves, it was 50%.

Figs. 3a and 3b show the relationship between accumulation of dry matter and accumulation of degree days (ACDD). The increase in DWT-L and DWT-ST with time cannot be explained by ACDD, since three separate response lines, one for each temperature, were obtained. This leads to the conclusion that the effect of temperature on the accumulation of dry matter was influenced by other factors, like the number of leaves or number of tillers. Calculation of the response to ACDD on a leaf or tiller basis, instead of on a whole plant basis, gave a linear regression with the following equations:

$$\text{DWT/leaf} = 0.07 + 0.0007 \text{ degree days } (r^2 = 0.879 \text{ } n = 22)$$

$$\text{DWT/tiller} = -0.46 + 0.02 \text{ degree days } (r^2 = 0.902 \text{ } n = 22)$$

Values are in g. DM.

The difference between the leaf and the tiller equation is due to stem elongation. ACDD was calculated assuming a threshold temperature of 13.5°C. Recalculation of the tiller equation using a threshold temperature of 14.5°C brings the regression line close to the origin (intercept = 0.07), which means that stem growth of hybrid Pennisetum starts at a higher temperature than leaf growth.

The changes in total dry weight with time is strongly related to SPER-L, the weight ratio between the stems and the leaves (Fig. 4). Plants weighing less than 75 g (equivalent to SPER-L of 1.0) contain mainly leaves. Most of the additional dry weight of plant weighing more than 75 g comes from the stem.

Fig. 3. The increase in dry weight of leaves (A) and of stems (B) as related to accumulation of degree days.
 □ 32/22(°C) △ 27/17(°C) + 22/12(°C)

Fig. 4. Relationship between total plant weight and stem/leaf weight ratio under three temperature regimes.
 □ 32/22(°C) △ 27/17(°C) + 22/12(°C)

Fig. 5. Relationship between stem weight and leaf weight under three temperature regimes

Fig. 5 shows the distribution of dry weight between leaves and stems. In the young plant there is only a gradual increase in stem weight whereas the weight of leaves increases rapidly. A massive accumulation of dry weight in the stem fraction begins about at the age of 4 weeks following cutting.

B. Digestibility

The changes occurring in leaf and stem digestibility with time are shown in Figs. 6a and 6b. Initially, both leaf and stem IVDMD are very high. The rate of decline in IVDMD of leaves with age was affected by temperature conditions. During the first 5 weeks of growth DIG-L declined by 10 and 2 % units under the 32/22 and 22/12°C temperature regimes, respectively. From the 5th week onward, only minor changes in leaf digestibility were evident in all the three temperature regimes. The decline in DIG-L with time seems to be related to two phenomena: firstly, the digestibility of the single leaf declines with advancing maturity, and, secondly under low temperature conditions a greater part of total leaf dry weight is contributed by leaves which have not yet reached full expansion, whereas under high temperature conditions relatively more leaves are fully mature or even senescing.

The changes in stem digestibility (DIG-ST) with time follow a different pattern (Fig. 6b). Young stem material, which consist mainly of leaf sheaths has a similar dry matter digestibility as that of young leaf blades of identical age. As long as the stems are young and physiologically immature, the decline in digestibility is slow, irrespective of the

Fig. 6. Relationship between leaf (A) and stem (B) digestibility and age as a function of temperature.

Fig. 7. The decline in whole plant digestibility as related to the accumulation of degree days.
 □ 32/22 (°C) Δ 27/17 (°C) + 22/12 (°C)

temperature. As can be seen in figure 6b, temperature conditions have a significant effect on the duration of the moderate decline in DIG-ST but not on its rate. Under the high temperature regime, a clear decline in DIG-ST commenced at the 4th week whereas under the low temperature regime, a similar decline began at the 6th week. The results indicate that when the stems reached a certain stage (not defined) of development the rate of DIG-ST decline was similar under all three temperature regimes. The overall rate of decline in digestibility was much greater in the stems than in the leaves. Since the rate of the DIG-ST response was similar under the different temperature regimes we suggest that temperature only indirectly affects stem digestibility. In contrast, the different pattern of response in the leaves as compared to the stems suggests that direct effect of temperature on leaf digestibility cannot be ignored. Since most of the influence of temperature on digestibility seems to be related to the developmental stage of the plant, it was thought that degree days may offer a reliable estimate of digestibility of the dry matter as shown in Fig. 7.

Digestibility of leaves differed from that of stems also in relation to dry matter content. Fig. 8 shows a curvilinear relationship between digestibility and DM content for the leaves (a) and a linear relationship for the stems (b). At all temperatures DIG-L decreased with increasing PDM-L up to 15%. No further decrease in DIG-L was found as PDM-L increased up to 23%. In contrast DIG-ST declined linearly with increasing PDM-ST.

C. Crude protein content

The crude protein content was higher in plants growing under the low temperature regime compared with the high temperature regime. It declined

Fig. 8. Relationship between leaf (A) and stem (B) digestibility and percentage of dry matter as function of temperature.
□ 32/22(°C) Δ 27/17(°C) + 22/12(°C)

Fig. 9. Relationship between leaf (A) and stem (B) crude protein and age as function of temperature.

Fig. 10. Relationship between crude protein content and dry weight of leaves (A) and stems (B) under three temperature regimes.
 □ 32/22(°C) Δ 27/17(°C) + 22/12(°C)

curvilinearly with time both in leaves and in stems (Figs. 9a, 9b), particularly during the first 4 weeks of growth.

The decrease in the crude protein content with the increase of leaf or stem weight (Figs. 10a, 10b) reflects a dilution effect, as structural carbohydrates accumulate relatively more with advancing maturity.

D. The relationship between dry matter digestibility and crude protein content.

In many instances, dry matter digestibility and crude protein content are closely related (Figs. 11a, 11b, 11c). In the leaves, digestibility increased linearly with crude protein content, its rate depending on temperature. In the stems the response was curvilinear and independent of temperature. Here, CP declined strongly in early stages of development, whereas IVDMD declined mainly during the later stages.

E. A morphological criterion of forage quality.

It is suggested that the number of expanded leaves per tiller can be used as basis for estimating forage quality in hybrid Pennisetum. The changes in the number of expanded leaves/tiller over a period of time and their relationship to the quality of the dry matter are presented in Figs. 12, 13, 14. The rate of leaf expansion was affected by growth temperature (Fig. 12). With a temperature combination of 27/17°C (the closest to 23°C, which is the average seasonal temperature at Bet Dagan), the number of expanded leaves/tiller increased with chronological age up to the 6th week of the growth cycle. At that time, a mean of 5 leaves per tiller were fully expanded. The further increase in total plant weight is therefore a result

Fig. 11. Relationship between digestibility and crude protein content of leaves (A), stems (B) and whole plant (C) as function of temperature.
 □ 32/22(°C) △ 27/17(°C)+22/12(°C)

Fig. 12. The change in number of expanded leaves/tiller over time as function of temperature.

Fig. 14. Relationship between number of expanded leaves/tiller and accumulated degree days over eight weeks of growth.

Fig. 13. The decline in digestibility (A) and crude protein (B) as related to number of expanded leaves/tiller under three temperature regimes.

□ 32/22(°C) Δ 27/17(°C) + 22/12(°C)

of an accumulation of dry matter mainly in stem tissue, which causes a strong decline in digestibility. There is a close relationship between the number of expanded leaves/tiller and IVDMD and CP. Figs. 13a and 13b show that this relationship is independent of the effect of temperature.

Accumulation of degree days is closely related to the rate of leaf development (Fig. 14). It can be seen that 400 degree days are required for the fifth leaf to reach full expansion. ACDD can be easily calculated from the known threshold temperature and measured day and night temperatures. Although it appears to be a reliable parameter for estimating IVDMD, CP and canopy structure, its use is restricted to the long days of spring and mid summer in which vegetative development is predominant. A listing of the regression equations for figures 1-14 is given in Table 5.

Table 5: Regression equations for the relationship between plant attributes as function of temperature.

Temperature	Variables ¹⁾		Regression	R ²	Figure No.
	(Y)	(X)			
1 2)	PDM-L	WEEK	$7.140 + 1.646x + 0.079x^2$	0.962	1a
2			$8.053 + 1.365x + 0.051x^2$	0.986	"
3			$7.339 + 2.331x - 0.117x^2$	0.950	"
1,2,3	PDM-ST	WEEK	$4.717 + 0.201x + 0.152x^2$	0.911	1b
1	DWT-L	WEEK	$-10.026 + 14.114x$	0.982	2a
2			$-12.604 + 11.736x$	0.975	"
3			$-7.479 + 7.184x$	0.964	"
1	DWT-ST	WEEK	$-20.547 + 10.109x + 2.587x^2$	0.978	2b
2			$2.145 - 6.149x + 3.375x^2$	0.967	"
3			$1.731 - 1.518x + 0.954x^2$	0.925	"
1	DWT-L	ACDD	$-10.026 + 0.170x$	0.982	3a
2			$-12.600 + 0.246x$	0.975	"
3			$-7.479 + 0.570x$	0.964	"
1	DWT-ST	ACDD	$-0.342 + 0.017x - 1.299x^2$	0.997	3b
2			$-0.652 + 0.026x - 3.024x^2$	0.989	"
3			$-0.531 + 0.071x - 0.0002x^2$	0.982	"
1,2,3	TOT-PLWT	SPER-L	$-8.508 + 41.666x + 43.701x^2$	0.964	4
1,2,3	DWT-ST	DWT-L	$0.011 + 0.054x + 0.022x^2$	0.987	5
1	DIG-L	WEEK	$86.125 - 8.998x + 1.450x^2 - 0.079x^3$	0.984	6a
2			$81.085 - 3.409x + 0.367x^2 + 0.016x^3$	0.984	"
3			$83.546 - 4.397x + 0.845x^2 - 0.054x^3$	0.883	"
1,2,3	DIG-TOT	ACDD	$72.229 - 0.028x$	0.966	7

1	DIG-L	PDM-L	$261.792 - 132.839x + 22.581x^2$	0.997	8a
2			$155.826 - 52.343x + 7.874x^2$	0.988	"
3			$171.249 - 66.597x + 11.576x^2$	0.786	"
1	DIG-ST	PDM-ST	$87.522 - 1.473 x$	0.955	8b
2			$84.445 - 0.943 x$	0.916	"
3			$82.942 - 0.501 x$	0.828	"
1	CP-L	WEEK	$32.130 - 5.808x + 0.380x^2$	0.986	9a
2			$34.287 - 5.357x + 0.304x^2$	0.992	"
3			$42.562 - 6.336x + 0.360x^2$	0.948	"
1	CP-ST	WEEK	$31.964 - 7.551x + 0.520x^2$	0.976	9b
2			$43.252 - 10.251x + 0.687x^2$	0.992	"
3			$52.805 - 10.123x + 0.594x^2$	0.994	"
1,2,3	CP-L	DWT-L	$28.553 - 0.379x + 0.001x^2$	0.972	10a
1,2,3	CP-ST	DWT-ST	$22.701 - 0.273x + 0.0009x^2$	0.877	10b
1	DIG-L	CP-L	$59.351 + 0.660x$	0.927	11a
2			$64.132 + 0.466x$	0.967	"
3			$71.124 + 0.253x$	0.509	"
1,2,3	DIG-ST	CP-ST	$13.693 + 0.875x - 6.280x^2$	0.921	11b
1	DIG-TOT	CP-TOT	$51.357 + 2.025x - 0.039x^2$	0.938	11c
2			$59.582 + 1.451x - 0.029x^2$	0.943	"
3			$62.703 + 1.303x - 0.027x^2$	0.913	"
1	EXPL-TIL	WEEK	$-0.384 + 1.710x - 0.111x^2$	0.937	12
2			$-0.979 + 1.584x - 0.111x^2$	0.950	"
3			$1.266 - 0.008x + 0.038x^2$	0.853	"
1,2,3	DIG-TOT	EXPL-TIL	$79.532 - 0.554x - 0.319x^2$	0.887	13a
1,2,3	CP-TOT	EXPL-TIL	$32.105 - 6.322x + 0.352x^2$	0.887	13b
1,2,3	EXPL-TIL	ACDD	$6.15(1 - e^{-0.00478 x})$	SD= 0.544	14

1) Variables are specified in Table 1.

2) Temperature 1 = 32/22 °C 2 = 27/17 °C 3 = 22/12 °C

PART 3. VEGETATIVE PROPAGATION OF HYBRID PENNISETUM

ABSTRACT

Hybrid Pennisetum is usually propagated vegetatively since no commercial amounts of seed are available. Aerial tillers make excellent propagating material because of the following:

1. The amount of propagation material which can be raised for this method from a unit of land, is approximately 25 times greater than that produced for the usual method in which stem cuttings are planted.
2. The establishment of the field is fast, and if the moisture regime is properly maintained tiller replacement is negligible.
3. Planting of aerial tillers can be easily mechanized.
4. The propagation material of hybrid Pennisetum can be stored at 12°C for approximately 30 days.

INTRODUCTION

Plants of hybrid Pennisetum are propagated vegetatively since no commercial amounts of seed are available. In countries where napiergrass is a common forage crop, stem cuttings are usually used for propagation which is a complicated and inefficient technique. It requires large amounts of planting material because the cuttings need to have at least two nodes each, and only the lower nodes of the stem are considered suitable for propagation. Furthermore, establishment is partial and replacements are

usually required. Also the period for establishment from stem cuttings is long.

RESULTS AND DISCUSSION

The use of aerial tillers for propagation

Aerial tillers appeared in autumn from almost every node along the stems which were left uncut since August. These tillers start to develop just before flowering of the main stem, remain small during the winter and start growing in the following spring. When they had formed approximately 5 leaves in May, and their basal diameter reached 5-7 mm they were carefully removed from the main stem so as not to damage the apex which is located at the base of the tiller. The aerial rootless tillers were stuck into the cultivated soil to a depth of approximately 3 cm. A suitable moisture regime was maintained by frequent sprinkling. Five days after planting, root intitiation was observed and establishment was more than 90%. The amount of propagation material which can be raised from a unit of land by this technique was estimated as 25 times greater than the ordinary method of using stem cuttings.

Mechanized planting

We tried mechanized planting similar to the method used routinely for bermuda grass swards, lawns etc. To the best of our knowledge this technique has not been employed for tall and coarse grasses such as napiergrass or its hybrids.

An experimental plot of 500 m² was cultivated to produce an undulating surface. In late May 20 x 1.8 m of a mature stand of hybrid 23AxN20 bearing aerial tillers was cut at 10 cm above soil level with a commercial mower (avoiding fine chopping). This operation resulted in plant segments between 10 - 20 cm long. This material was then spread with a manure distributor over the soil surface allowing for approximately 15 segments to cover 1 m². The soil was rolled twice to ensure good contact between the segments and the soil and was immediately irrigated.

Light irrigations were given twice a day for a further 3 weeks to maintain favorable moisture conditions in the upper soil layer. The number of established plants, defined by the growth of new leaves was counted 15 and 23 days after planting. On day 15, only 3 ± 0.3 plants m² were established whereas one week later there were 5.8 ± 0.5 plants m². No further counts were made, since a density of 5.8 plants m² is considered sufficient for maximum dry matter production. It was concluded that mechanized planting as described above, can be a reliable and efficient technique for the establishment of hybrid Pennisetum fields.

Storage of the propagation material

A large-scale method of propagation requires the storage of plant material. An experiment was conducted to investigate the temperature conditions and time duration for the storage of unrooted propagation material of hybrid 23AxN23 and of napier N23. The experiment with hybrid 23 was conducted during May-June when the aerial tillers were relatively young, whereas the experiment with napiergrass started in September and included well developed tillers.

The plant material was stored in two ways as:

1. Aerial tillers attached to the main stem, and
2. Detached tillers

The hybrid was stored at 6, 10 or 12°C, and the napiergrass material was stored at 6, 8 or 12°C. The relative humidity in the store rooms was maintained at 70%. On the day of storage, and at different intervals afterwards, 20 unrooted tillers from each treatment were planted in the glasshouse under suitable growing condition. The aerial tillers stored attached were separated from the stem just before planting. One week after each planting, tiller establishment was recorded. A control plot was planted with tillers that were not stored previously. The results are shown in Figs. 1 and 2.

The optimal storage temperature for hybrid tillers was 12°C irrespective of whether they were detached or attached to the stems. At this temperature they maintained excellent viability even 30 days after being stored. Detached tillers of napiergrass remained more viable after approximately 30 days in storage than the attached tillers.

The dm% of the detached and the attached tillers (after being separated from the stems) was determined 30 days after storage was started.

The results are presented in Table 1.

Fig. 1. Effect of temperature and storage method on the establishment of hybrid Pennisetum (23AXN23) tillers.

Fig. 2. Effect of temperature and storage method on the establishment of Napier grass (N23) tillers.

Table 1. The effect of storage conditions on percentage of dry matter in napiergrass tillers . Means of 20 tillers.

Temperature (°C)	Dry matter (%)	
	Attached tillers	Detached tillers
12	77.6	27.5
8	61.1	39.9
6	58.8	33.3

The reason for storing aerial tillers attached to the stems was that the stem, may satisfy the demand of the tillers for moisture during storage. This seems possible as long as the moisture content of the stems is higher than that of the attached tillers (i.e. when an immature stem is stored). However, if the stem is more mature and its moisture content is lower than that of the attached tillers, it may well withdraw moisture instead of supplying it to the tillers. It is suggested that this was the reason for the high dm% of the attached tillers of napiergrass which in turn caused a decrease in their viability. It is concluded that mature material should be stored as detached tillers whereas immature ones can also be stored successfully with aerial tillers attached to the stem.

PART 4. MAXIMISING PRODUCTION OF DIGESTIBLE DRY MATTER

ABSTRACT

Field experiments in which Pennisetum hybrids were subjected to several cutting intervals and irrigation regimes were conducted. A very high mean crop growth rate of $362 \text{ kg ha}^{-1} \text{ day}^{-1}$ was attained during 10 weeks of undisturbed growth of two Pennisetum hybrids under 'no stress' management conditions in a field experiment at Bet Dagan.

Both hybrids are characterized by early stem elongation, and a wide range of tiller size during later development.

Early stem elongation reduces the rate of regrowth after cutting, already at approximately 40 days of age. The sensitivity of hybrid Pennisetum to cutting is expressed in the negative relationship between the number of cuts per season and the mean crop growth rate.

The effect of irrigation regime on digestibility was mediated by its effect on the morphological structure of the canopy. It was found that increased digestibility due to irrigation can only be obtained at the expense of dry matter accumulation.

INTRODUCTION

As a rule, multi-cut grasses are mowed at a relatively immature stage for a number of reasons, the most important being, the need to obtain a high digestibility of the dry matter, and good regrowth. Determination of

optimum cutting dates requires information on growth and digestibility curves as well as on regrowth over a wide range of time.

In order to obtain data on Pennisetum hybrids, we ran a set of trials in which the grass was allowed to grow for different periods between successive harvests and under various irrigation regimes.

A. UNDISTURBED GROWTH

MATERIAL AND METHODS

A 0.5 ha field experiment was established in summer 1981 from aerial tillers which were planted at a distance of 50x50 cm between plants. The field was cut twice with a commercial mower in spring 1982. The second cut was made on June 21, 4 weeks before the experiment commenced, to ensure good regrowth. The experiment consisted of two hybrids; 23A x N17 and 23A x N20, and production was measured weekly for a period of 10 weeks commencing on the day of cutting.

The experiment had a randomized block design and was replicated three times. Each block consisted of 18, 10x4m plots from which an area of 18m² was cut and weighed.

The plots were sprinkle irrigated once a week with an average of 7mm water day⁻¹. Nitrogen, as liquid NH₄NO₃ was supplied through the irrigation system at a rate of 5 kg N ha⁻¹ day⁻¹. Superphosphate at a rate of 1000 kg ha⁻¹, and 500 kg ha⁻¹ potassium chloride were supplied before planting.

Every week between July 7 and August 30 two plots in each block were mowed, one for each hybrid. At each cutting date, two plants from each plot

were sampled randomly for determining canopy structure and for chemical analyses.

The plant material was separated into 4 fractions:

- A. Leaf blades of nonelongated (vegetative) tillers
- B. Leaf sheaths of non-elongated tillers.
- C. Leaf blades of elongated tillers.
- D. Stems + Leaf sheaths of elongated tillers.

The stems were divided into groups according to the number of nodes. The samples were oven dried at 70°C, weighed and analyzed for in vitro dry matter digestibility (IVDMD) and crude protein (CP).

RESULTS AND DISCUSSION

Distribution of dry matter, digestibility and crude protein

Regrowth after the initial cut was excellent due to the relatively short precutting period. The plants of both hybrids reached their maximum growth rate approximately 3 weeks after cutting. Between the 3rd and the 10th week, the increase in dry weight was almost linear (Fig.1). After 10 weeks of growth, the total yields were 25.0 and 26.4 t DM ha⁻¹ corresponding to 357 and 377 kg ha⁻¹ day⁻¹ for hybrid 17 and 20, respectively.

No differences in either IVDMD or CP were detected between the hybrids. The overall change in digestibility amounted to 20 % units, ranging from 63% in the 3rd week to 43% at the end of the 10th week of growth. The decrease in IVDMD can be considered either linear

Fig. 1. Yield increase over 7 weeks of undisturbed growth.

□ total yield	$y = -5.08 + 2.99x$	$r^2 = 0.994$
△ digestible yield	$y = -0.57 + 1.23x$	$r^2 = 0.978$
+ crude protein yield	$y = 0.87 + 0.26x$	$r^2 = 0.960$

Fig. 2. Decline in digestibility over time in two hybrids.

□ 23AXN17
△ 23AXN20

Fig. 3. Decline in crude protein over time in two hybrids.

□ 23AXN17
△ 23AXN20

Fig. 4. Distribution of dry weight and digestible dry weight between leaves and stems over 7 weeks of undisturbed growth.

□, + leaf, stem dry weight
△, × leaf, stem digestible dry weight

($Y_{(3-10wk)} = 70.9 - 2.8x$ $r^2 = 0.958$) or as a two phase decline, before and after the 5th week (Fig. 2). In both cases, the rate of decrease in digestibility was very rapid. This resulted in a mean daily increment of 175 kg ha^{-1} of digestible dry matter (Fig. 1).

The decline in CP over time was also in two phase (Fig. 3). Between the 3rd and the 7th week of growth there was a decline of 8% units in CP. Between the 7th and the 10th week, the period which appears to be unsuitable for grazing or cutting, the decline in CP was less marked or even negligible in hybrid 20.

The distribution of dry matter and of digestible dry matter between leaves and stems is shown in Fig. 4. The accumulation of both was linear in the stems and curvi linear in the leaves. Weight accumulation in the young the young plant (up to the 5th week) was similar in leaves and stems. During the course of ontogenetic development the distribution of dry matter and digestible dry matter changes steadily in favor of the stems. The change in digestible dry matter in the leaves of a seven-week old or an older plant is negligible. After the 7th week, the increase in young, highly digestible leaf blade tissue is compensated by ageing or even death of lower leaves which metabolize for a relatively long period under very deep shade. Leaf weight ratio (LWT-R, i.e. weight of leaf blades as a percentage of total weight) for the dry matter, and digestible yield declined similarly until the 5th week of growth. Later on, LWT-R for digestible yield declined moderately in comparison with that of dry matter yield (Fig. 5). This was due to the differences between leaf and stem IVDMD over the experimental period as shown in Fig. 6. The digestibility of the leaf blades declined by 10% units and that of the stems by 21% units between the 3rd and the 10th week. The difference

Fig. 5. The change in the relative weight and relative digestible weight of the leaves during undisturbed growth.

● DWT
△ DIG-DWT

Fig. 6. Decline in digestibility of leaves (△) and stems (x) over time.

Fig. 7. Decline in crude protein of leaves (△) and stems (x) over time.

between the two plant parts increased with advancing maturity. A similar, but less marked pattern was found for the changes in CP (Fig. 7). Crude protein content was very high until the 4th week in both young leaves and stems. After that, CP content declined sharply but at different rates which later resulted in 2.5% units difference in favor of the leaf blades. From the 7th week onward, CP content was constant at a relatively low level of approximately 10 and 13% in the leaves and the stems, respectively.

The canopy structure

The number of stems, as a percentage of total number of tillers increased in both hybrids between the 3rd and the 7th week from about 30 to 90%, after which it remained constant (Fig. 8).

Fig. 8. Increase in stem percentage during 7 weeks of undisturbed growth in two hybrids.

■ 23AXN17
 ▲ 23AXN20

Fig. 9. Distribution of dry weight between nonelongated (Δ) and elongated tillers (x) total yield (□)

Fig. 10. Distribution of elongated tillers between the 3rd and 10th week of age according to the number of nodes/stem in two pennisetum hybrids.

□ 23AXN17
△ 23AXN20

Approximately 7% of the tillers were vegetative after 7 weeks of growth. It is assumed that this group of tillers was initiated relatively late, when the rest of tillers were already high and dense. Under these conditions, the late developing vegetative tillers have only a small chance to complete their ontogenesis.

The mean dry weight of an elongated tiller increased with age and reached a value of 20 g. In contrast, the mean weight of a vegetative tiller was not more than $1.1\text{g} \pm 0.3$. It is therefore obvious that elongated tillers contribute decisively to the total yield, whereas that of vegetative tillers is negligible (Fig. 9).

The uniformity of tiller size distribution in the canopy is of practical importance with regard to the optimum date for harvesting. Fig. 10 show that tiller uniformity decreased with time after cutting. Tiller uniformity would be enhanced if stem elongation could be retarded, either by breeding or agrotechnically. However, this aspect was not investigated in the present study. A further discussion on this aspect appears in part 5 of the report.

B. RESPONSE TO CUTTING

INTRODUCTION

Production of forage grasses is strongly influenced by the response of the plants to cutting or grazing. Several field experiments were carried out in which the hybrids were subjected to different cutting intervals. Unfortunately, all field experiments but one could not be continued for a second season since most of the plants died during the exceptionally long, wet and cold winter.

DEVELOPMENT, DRY WEIGHT DISTRIBUTION AND REGROWTH AFTER CUTTING

The canopy structure of hybrids 17 and 20 was recorded in the field at kibbutz Gvat located in the Jesreel valley, in plots planted at a distance of 50 x 50 cm. Measurements were taken from 50 plants of each hybrid. Every week, 5 plants of each hybrid were selected at random, and cut 10 cm above ground level. The herbage was hand separated into non-elongating and elongating tillers and weighed. One week after each cutting, the number of regrowing tillers was counted and regrowth was expressed as the number of regrowing tillers relative to the number of tillers on the day of cutting.

The development of the canopy of the two hybrids was similar. The number of non-elongating tillers increased rapidly after cutting and reached its maximum at the fifth week of growth (Fig. 1).

Fig. 1. Canopy structure and regrowing tillers as related to time after cutting (average for hybrids 23AXN17 and 23AXN20).

Fig. 2. Tiller weight distribution in hybrid *Pennisetum* related to time after cutting (average for hybrids 23AXN17 and 23AXN20).

Stem elongation started during the 3rd week and increased moderately until the fifth week, from then onwards the number of elongated stems increased curvilinearly and reached 97% of total tillers at the 10th week. No further increase in total number of tillers *per* plant was found after the 7th week.

The accumulation of herbage and its tiller weight distribution is presented in Fig. 2. The figure shows that herbage accumulation follows a similar pattern as the rate of tiller development.

Plants which were cut at an early stage of development (less than 4 weeks of age) regrew faster than plants cut at a later developmental stage. In 4-week-old plants, not less than 83% of the cut tillers were capable of regrowth after cutting (Fig. 1). In plants older than 4 weeks, the rate of regrowth declined by 16% for every week of deferment in cutting.

THE EFFECT OF PLANT DENSITY AND CUTTING FREQUENCY ON YIELD AND DIGESTIBILITY OF TWO PENNISETUM HYBRIDS

In another experiment, aerial tillers of hybrids 17 and 20 were planted at two densities: 3 or 6 plants m^2 in the field at kibbutz Nachsholim located in the coastal plain.

The experiment was a split-plot design with 4 replications. In the first season the plots were cut after either 5 or 7 weeks, whereas in the second season an attempt was made to cut the plants according to a morphological parameter for stage of development.

Both hybrids irrespective of planting density, produced similar dry matter yields during the first season (Table 1).

Table 1. The effect of planting density and cutting interval on dry matter yield (ton ha⁻¹) of two pennisetum hybrids

Harvest date	Growing period (weeks)	Hybrid			
		23AXN17	23AXN17	23AXN20	23AXN20
		Planting density (plants m ⁻²)			
		3	6	3	6
20.7.82	7	11.35±.95	11.64±.75	12.20±1.33	12.85±1.42
24.8.82	5	4.30±.55	4.37±.40	4.46±.50	4.66±.21
29.9.82	5	4.91±.26	5.00±.20	5.24±.36	4.86±.19
Total	17	20.56	21.01	21.89	22.37
20.7.82	7	11.35±.95	11.64±.75	12.20±1.33	12.85±1.42
7.9.82	7	9.14±.40	7.29±.50	8.04±.58	7.53±.51
Total	14	20.49	18.93	20.24	20.38

Table 2. The effect of planting density and cutting interval on in vitro dry matter digestibility of two pennisetum hybrids.

Harvest date	Growing period (weeks)	Hybrid			
		23AXN17	23AXN17	23AXN20	23AXN20
		Planting density (plants m ⁻²)			
		3	6	3	6
24.8.82	5	56.8±0.6	58.7±1.2	59.5±0.1	57.9±1.1
28.9.82	5	62.7±1.3	66.2±1.4	60.7±1.1	63.2±1.7
20.7.82	7	54.4±0.3	50.0±1.1	53.4±1.3	50.3±0.6
7.9.82	7	54.9±0.9	57.1±1.3	57.1±0.8	53.5±0.9

A growth period of 7 weeks followed by two 5 week cycles produced a total dry matter yield similar to that obtained from two growth periods of 7 weeks each. This result shows the sensitivity of hybrid Pennisetum to defoliation even at a relatively young age of 5 weeks when the canopy is divided more or less equally between elongating and non-elongating tillers. It should be noted that this occurred in both hybrids, which, although different in their morphology as mentioned earlier, are not different with regard to the initiation and the rate of stem elongation.

During the second experimental season the length of the cutting intervals were different. It was planned to cut the sward at two stages of growth: (a) when 10% or (b) 50% of the tillers had elongated. This unfortunately could not be done since the transition from a vegetative to an elongated tiller was unexpectedly rapid.

The digestibility of the dry matter was found to be exceptionally low. The mean IVDMD was 57.2 and 54.5% for the first and the second growing seasons respectively, (Table 2). No main effects were found either for the hybrids or the planting density. Plant age was the major factor determining the digestibility of the plants. The response to cutting will be further discussed in part 5 of this report.

C. RESPONSE TO IRRIGATION

INTRODUCTION

Economically, the use of irrigation water for the growing of forage crops in Israel deserves careful consideration. C_4 plants have superior water use efficiency (WUE) in comparison with C_3 plants. Within the C_4 group, the perennial, multi-cut grasses have a lower WUE than annual, single cut crops such as maize or pearl millet, since root functioning in the former is temporarily reduced. Furthermore multi-cut grasses have a shallower root system than single cut crops and may require more frequent irrigations to achieve maximum yields.

The aim of the present study was to determine whether there is a difference between the WUE in the production of dry matter and of digestible dry matter under different irrigation regimes.

MATERIALS AND METHODS

Plots of 12x12m each of hybrid 23A x N23 were established at Bet Dagan from aerial tillers in a factorial, completely randomized design with 4 replications. Empty border plots of identical size surrounded each of the experimental plots. The irrigation water was applied by sprinklers placed at the corners of each plot. Three irrigation frequencies at two different saturation depths (to field capacity) were tested and are listed in Table 1.

Table 1. The irrigation treatments

Treatment	Irrigation frequency	Saturation depth
No.		(cm)
1	Twice a week	0-60
2	"	0-90
3	Once a week	0-60
4	"	0-90
5	Every fortnight	0-60
6	"	0-90

Soil moisture was measured twice a week in each plot using a neutron scattering probe to a depth of 180 cm. The first measurement was made on the day of irrigation of treatments 3 and 4, and the second, 48 h later. The amount of water required to reach field capacity at the depths listed above was calculated using a calibration curve. The amounts of water applied to treatments 1 and 2 were equally divided between the first and the second irrigations.

Nitrogen as liquid NH_4NO_3 was supplied through the irrigation system proportionally to the amount of water applied. The N content in the irrigation water was kept at a constant concentration of 120 ppm.

The field was planted in summer 1981 and the plots were cut once in that year. In the spring of the next growing season the plots were irrigated once a week at a rate of 70% of a class A pan evaporation and cut twice during 70 days after which a reasonably uniform stand was obtained.

The irrigation treatments were applied immediately afterwards and the plots were harvested on day 28 and day 63.

From the end of the second cut onwards water was applied uniformly to all plots in order to eliminate the possible carry-over effect from differential irrigation treatments into the second growing season. The experiment had to be terminated in spring 1983 due to severe frost damage and plant death during the 1982/83 winter season. Results are presented from one season only.

WUE is expressed as kg DM/mm water.

RESULTS AND DISCUSSION

Table 2. Amounts of irrigation water (mm) applied.

Irrigation frequency	Twice weekly		Weekly		Fortnightly	
	0-60	0-90	0-60	0-90	0-60	0-90
1st cutting	155	232	180	263	173	172
2nd cutting	132	245	210	223	170	170
Total	387	477	390	486	343	342
mm/day	6.1	7.6	6.2	7.7	5.4	5.4

The analysis of variance for the main effects and their interactions is presented in Table 3.

Table 3. Analysis of variance of the main effects and their interactions.

Source	DM ¹⁾	IVDMD	PDM	CP	DIGTOT	WUE
Depth	NS	NS	*	*	NS	***
Frequency	NS	NS	***	NS	NS	***
Cut	*	NS	***	NS	***	***
CutXDepth	*	**	NS	***	NS	***
CutXFrequency	***	***	***	NS	**	***
DepthXFrequency	NS	NS	NS	NS	NS	*

* ** *** Significant at 0.05, 0.01 and 0.001 probability level respectively.

1) variables are specified in Table 1 p. 76

Depth of irrigation had no effect on dry matter yield, nor on digestibility. Dry matter percentage (PDM), CP content and WUE were affected by depth of irrigation mainly because of the greater amount of water that was applied. Similar conclusions, except for the effect on CP content can be drawn for the effect of the irrigation frequency treatments.

In contrast, dry matter and digestible dry matter yields were affected only by the cutting regime. PDM and WUE were the only variables that were significantly affected by the frequency, depth and cutting factors. There was no interaction between depth and frequency of irrigation in their effect on any of the variables listed in table 3 except WUE.

Since the cutting interacts with either depth or frequency of irrigation in its effect on DM yield, each growth period was analysed separately (Table 4).

Table 4. The effect of irrigation regimes on yield, quality and water use efficiency of hybrid pennisetum.

Treatments No.	Freq. ₂	Depth (cm)	DM (t ha ⁻¹)	PDM (%)	IVDMD (%)	DIG-DM (t ha ⁻¹)	CP (%)	WUE ₁ (kg mm ⁻¹)
FIRST CUTTING								
1	2	0-60	5.7a ¹⁾	10.2b	61.0c	3.5a	16.3c	3.7a
2	2	0-90	5.5ab	10.2b	63.8bc	3.5a	18.1bc	2.4c
3	1	0-60	5.4ab	10.3b	54.9ab	3.5a	18.1bc	3.0b
4	1	0-90	4.5bc	11.0ab	66.6ab	2.9b	20.0a	1.7d
5	0.5	0-60	4.7bc	11.5a	65.2ab	3.1ab	18.8ab	2.7bc
6	0.5	0-90	3.9c	11.8a	67.6a	2.6b	17.5bc	2.2cd
SECOND CUTTING								
1	2	0-60	3.7b	11.9c	65.8a	2.4a	20.6a	1.6b
2	2	0-90	3.8b	11.8c	65.2a	2.4a	18.8a	1.5b
3	1	0-60	4.0ab	11.1c	64.3ab	2.5a	2.0a	1.9b
4	1	0-90	4.3ab	11.7c	62.5ab	2.7a	16.9b	1.9b
5	0.5	0-60	4.5ab	13.2b	62.9ab	2.8a	20.6a	2.6a
6	0.5	0-90	5.0a	15.0a	60.9b	3.0a	16.2b	2.9a
TOTAL								
1	2	0-60	9.4a	11.0c	63.4a	5.9a	18.8b	2.6a
2	2	0-90	9.3a	11.0c	64.5a	5.9a	18.8b	2.0b
3	1	0-60	9.4a	10.7c	64.6a	6.0a	19.4a	2.4a
4	1	0-90	8.8a	11.3c	64.5a	5.6a	18.1ab	1.8b
5	0.5	0-60	9.2a	12.4b	64.1a	5.9a	19.4a	2.7a
6	0.5	0-90	8.9a	13.4a	64.2a	5.6a	16.9b	2.6a

1) Values in columns followed by the same letter are not significantly different (p=0.05) according to Duncan's Multiple Range test.

2) No. of irrigations per week.

In the first cutting, higher dry matter yields were obtained for the frequent irrigation treatments than for the less frequent ones. However in the second cutting, the results were reversed, resulting in non-significant differences in total dry matter and digestible yields of both cuttings between all the treatments.

Cutting and depth of irrigation, as well as cutting and frequency of irrigation interacted also in their effect on the digestibility of the grass. In the first harvest, IVDMD was approximately 4% units higher in plants irrigated every fortnight than in those irrigated twice a week. Due to the effect of cutting, IVDMD of the grass in the second harvest was lowest in the former and highest in the latter. The result from the interactions mentioned above was that WUE for DM production was linearly related to WUE for production of digestible dry matter.

The regressions between IVDMD (y) and DM yield (x) (in t ha⁻¹) were negative as shown in the following equations:

$$Y \text{ (1st cutting)} = 78.7 - 0.027 x \quad r^2 = 0.765 \quad n = 24)$$

$$Y \text{ (2nd cutting)} = 78.5 - 0.035 x \quad r^2 = 0.704 \quad n = 24)$$

The regression equation for both cuttings indicate that any gain in digestibility due to irrigation regime is obtained at the expense of dry matter yield.

PART 5 : MODELLING OF REGROWTH

THE RELATIONSHIP BETWEEN CANOPY STRUCTURE, DIGESTIBILITY
AND REGROWTH AFTER DEFOLIATION IN HYBRID PENNISETUM.

ABSTRACT

The relationship between canopy structure (in terms of tiller number distribution according to length) and re-growth after defoliation and digestibility was studied of the culmed-tiller producing tropical grass hybrid pennisetum (Pennisetum purpureum x P. americanum). A simulation model called SIMPIL, based on the experimental results and on concepts developed for the sward-forming tropical Rhodes grass (Dayan et al., 1981), was able to predict satisfactorily the accumulation of dry matter, tiller number, and canopy structure following defoliation.

The re-growth capability of tillers depended on the apical distance (i.e. the distance measured between the ligule of the last fully-expanded leaf and the apical meristem), the cutting height and the distribution of tiller lengths. The rate of the initial re-growth of intact tillers depended on the amount of residual leaf mass left as stubble on the field, whereas new tiller growth from decapitated tillers depended on the number of basal buds. Growth was monitored through a simple function of irradiance, temperature and light extinction in the canopy; the latter analysed in terms of tiller length distribution.

Under optimal growth conditions, with respect to water and nutrient supply, the maximum crop growth rate of the canopy was approximately $300 \text{ kg ha}^{-1}\text{day}^{-1}$. The regrowth capability of plants cut after 3 weeks of growth was higher than that of plants cut after 6 weeks of growth. The delay in the immediate re-growth of the older canopy caused the dry matter yield after 6 weeks of growth to be similar to the total yields obtained from 2 cycles of growth from canopies cut at intervals of 3 weeks each.

Canopy digestibility decreased with time, due mainly to the development of tall tillers of low digestibility. However, it was found that the digestibility of small tillers in an older canopy was lower than that of tillers of the same physiological age in a young canopy, and was similar to the digestibility of the tall tillers. This phenomenon was analyzed in terms of the tiller dynamics of a canopy and was explained by the adverse effect of shading on the digestibility of the small tillers. These findings precluded the prediction of canopy digestibility as part of the simulation model.

INTRODUCTION

The typical curve of the dry matter accumulation of a crop follows a sigmoid shape (Charles-Edwards, 1982). Following sowing (or cutting), the growth rate is exponential, as long as environmental factors are not limiting growth. With the closing of the canopy resulting in full light interception, the growth rate remains constant and depends on the amount of incoming radiation. Dry matter accumulation during this phase is linear. Eventually the growth rate decreases, usually when flowering is reached, when no new leaves are produced or if old plant tissue dies and decomposes.

Under optimal growing conditions the yield obtained at the end of a growth period is determined on the one hand by the amount of incoming radiation, which determines the maximum crop growth rate during the period of linear growth, and on the other hand by the length of the period of linear growth.

Especially in multi-cut forage grasses like hybrid pennisetum, the length of the period of exponential growth is decisive in determining the total seasonal yield, because exponential growth recurs after each harvest and may reach a sizeable proportion of the seasonal growth period. The length of the exponential phase of growth depends on the canopy structure at the time of defoliation. When the canopy is composed of vegetative tillers, following a short cutting interval, the re-growth is rapid, and the exponential phase

is relatively short. On the other hand, when the canopy is mainly composed of elongated tillers, following a long cutting interval, the re-growth is slow, extending the period of exponential growth. The greater the proportion of time of the entire season that the canopy is in the exponential phase relative to the linear phase of growth, the lower the total seasonal yield.

The aim of this study was to investigate the relationship between the canopy structure and the re-growth after defoliation of hybrid pennisetum. Since in forage management not only quantity is needed but also quality, the relationship between canopy structure and in vitro dry matter digestibility (associated with nutritional quality) was also investigated. Exploring these relationships should enable decision making on the optimum dates of cutting with the aim to attain maximum seasonal yields of high nutritive value.

LITERATURE REVIEW

3.1 Growth Of Grasses

3.1.1 Morphology

The grass plant is an aggregate of identical units called shoots or tillers (Fig. 1). A tiller consists of a stem made up of nodes between which is a region of meristematic tissue called the internode. Each node bears a leaf, consisting of a leafsheath and a leafblade. At the junction between the leafsheath and the leafblade is a membranous structure called the ligule. Each node also bears one axillary, or lateral bud, called thus because it is located in the axil between the node and the leaf sheath (Langer, 1972).

Just above the terminal node is the stem apex where new nodes, leaves and axillary buds are initiated in acropetal succession. In the vegetative plant the nodes are tightly compacted, and the stem apex is near the soil surface. Upon floral induction the uppermost internodes elongate and the apical meristem is raised above the soil surface. The basal internodes remain short, and axillary buds or tillers associated with them are called basal buds or basal tillers, to differentiate from buds or tillers which raise with the expanding internodes. The latter are termed aerial buds or aerial tillers. In tropical grasses the process of internode elongation also occurs without floral induction (Langer,

Vegetative phase

Stem apex at ground level.
No stem production. Apex
not removed by cutting.
Unlimited tillering from
axillary buds.

Stem-elongation phase

Apex removed by cutting.
Further tillering limited
to development from dormant
basal buds.

Fig. 1: The morphology of a grass plant. Adapted from Jewiss (1972).

1972) and elongating tillers are called culmed (Hyder, 1972).

Each axillary bud, after its formation, can continue development to form a tiller. Tillering refers to the production of externally visible tillers (Jewiss, 1972). Not all buds form tillers and are then referred to as being inhibited (Mitchell, 1953), or dormant.

The first shoot of the plant is termed the main tiller. The axillary buds of the main tiller may produce shoots, which are designated primary tillers. These in turn may bear subsidiary shoots termed secondary tillers, and so on. A hierarchy of tillers differing in age and size is thus formed, which are interconnected at their base by vascular tissue (Langer, 1972).

The tillers of hybrid pennisetum may reach a height of 4-5m, with fully expanded leaves reaching over 1m long (Muldoon & Pearson, 1979c). Stems elongate soon after their appearance without floral induction. Plants usually do not produce rhizomes or stolons (ibid).

3.1.2 Physiology

The growth rate of a grass plant is determined by the rate of tiller initiation and the rate of growth of the individual tillers.

The rate of tiller production depends on both internal and external factors. Internal factors include genotypic and

apical dominance effects. An axillary bud does not form a tiller unless one or more fully expanded leaves (depending upon the species) are present above it (Mitchell, 1953; Langer, 1972). Also, when the stem internodes expand, tiller formation is stopped (Jewiss, 1972).

The external factors affect tiller initiation in part through their effect on the rate of leaf production. Since tillers are formed from buds in the axils of the leaves, the rate of tillering is limited by the rate of leaf production (Booyesen et al., 1963). Under optimal conditions, and when the plant is in the vegetative stage, the two rates are equal (Youngner et al., 1976).

Tillering is reduced by low light intensity, much more so than leaf production, and appears to be dependent mainly upon total radiant energy (Langer, 1972). Total shoot production also decreases with shading (Davis & Laude, 1964).

Higher temperatures increase leaf production rates. In temperate species, tiller production does not increase as much with temperature as leaf production, since tiller production has a lower optimum temperature than leaf production (Langer, 1972). In subtropical grasses tillering increases with leaf production rates (Ivory & Whiteman, 1978). In both cases total shoot production increases with temperature.

In hybrid pennisetum, a new tiller is not initiated on a parent tiller unless at least 6 leaves have appeared above the node of tiller origin. (Pearson, 1975). Tillering rate

per plant was at an optimum between 21/17 and 27/22C (day/night), and decreased with higher temperatures (Muldoon & Pearson, 1979a). Since leaf production rates per tiller, and thus the number of potential tillering sites initiated, did not decrease with temperature, the decrease in total tiller number per plant is probably due to the inhibiting effect of stem elongation on tiller production, as leaf production rates per tiller did not decrease with temperature.

3.1.3 Tiller competition

Donald (1963) defined competition to occur "...when each of two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate supply of the factor or thing is below the combined demand of the organisms." Where water and minerals are in adequate supply, light becomes the sole limiting factor to production.

As plants in a canopy develop, the biomass produced becomes limited by the availability of resources, and a process of mutual interference between them sets in depending on plant size and distance apart (Harper, 1978). The limiting resources are then shared, with a resultant reduction in individual plant development and an increasing number of dying plants (Aikman & Watkinson, 1980).

In grasses each plant consists of a number of tillers connected between each other by vascular tissue. In wholly

vegetative plants growing under conditions without environmental stress, large tillers divert assimilates to smaller tillers (Quinlan & Sagar; Ong et al., 1978; Smith & Rogan, 1980). However, when the entire plant is shaded or under nutrient stress no assimilate diversion takes place (Ong et al., 1978), and the smallest or youngest tillers are the first to die (Ong, 1978; Shih & Gascho, 1980).

3.1.4 Re-growth after defoliation

Cutting when the plant is in the vegetative stage removes only leaf material; subsequent re-growth arises from the continued leaf production from the stem apex and from the axillary meristems. However, during stem elongation the apex is lifted above the ground level, and cutting may remove part of the stem including the apex. Re-growth then depends on the undamaged axillary tillers in the axils of leaves below the cutting height. Since tillering is inhibited during stem elongation, no axillary tillers may be present, and re-growth then depends solely on the development of the inhibited axillary buds (Jewiss, 1972).

The main factor, therefore, which affects tiller re-growth is the fate of the stem apex at defoliation. However, since it has been observed that not all vegetative tillers re-grow, additional causes have been suggested, e.g. the sudden change in micro-climatological conditions (Williams, 1970), or the physiological shock following the

drastic change in the root:shoot ratio (Teel, 1962; MacLeod, 1965). Another possibility is that these non-regrowing tillers might have been yet incapable of independent growth (Marshall & Sagar, 1968). These tillers are often already dead at the moment of cutting, especially when the sward is in the reproductive stage (Langer et al., 1964).

The re-growth of the canopy thus depends on the number of vegetative tillers capable of re-growth following defoliation, and on the number of new tillers initiated. The level of carbohydrate-reserves in the stubble present may also be of importance, as these supply the assimilates required for initial growth (May, 1960).

3.2 Modelling Of Re-growth

When a crop is defoliated several times during the season the effect of each harvest on subsequent re-growth must be taken into account. Edelsten & Corral (1979) did this in a simple manner in a regression model by relating the length of the exponential phase to the amount of herbage harvested at the previous cut. Another means was by considering a certain proportion of the stubble weight as reserve assimilates and redistributing this into new leaf weight following defoliation, and making this the initial weight for the next simulation period (Sheehy et al., 1979).

Dayan et al. (1981), working with Rhodes grass, used a more realistic approach by taking into account the number,

size, and phenological state of the tillers present at the time of cutting and analyzing the effect of defoliation on tillers depending on their phenological stage. Muldoon (1979) reported a simple model to predict yields of hybrid pennisetum cut at 6-week intervals based on growth as related to meteorological inputs only, without considering, however, the effect of the precutting history on re-growth.

3.3 Digestibility Of Grasses

The quality of a forage crop is usually assessed on a whole-herbage basis, although there are great differences in quality between the various plant parts making up the herbage (Hacker & Minson, 1981). Although forage quality is associated not only with digestibility but also with palatability, the contents of crude protein, metabolizable energy, fiber, ash etc., we limit ourselves to in vitro dry matter digestibility (in short, digestibility) only, a commonly used and convenient parameter (Tilley & Terry, 1963).

The digestibility of plant tissue is generally related to its anatomy and chemical composition. Cutin (Monson et al., 1972), which makes up the cuticle, and lignin (Hanna et al., 1973) are indigestible, so that the epidermis, xylem and sclerenchyma fibers are poorly digested. On the other hand, mesophyll tissue is readily digestible (ibid), unless protected by the cuticle or lignified tissue.

The digestibility of leafblades, when compared at the moment of full expansion, decreases with the level of insert on the stem, which is associated with an increase in lignin content (Deinum, 1976; Wilson, 1976). With leaf age from the moment of full expansion the digestibility decreases, being more marked in the lower insert leaves, although the rate is low compared to other factors such as level of insert or temperature (ibid). The leafsheath behaves similarly to the blade (Wilson, 1976).

Higher temperatures cause a sharp drop in leaf digestibility and enhance the age effect. These results are related to the effect of temperature on lignification of the tissues (Deinum, 1976). Stem digestibility is similarly affected (Deinum & Dirven, 1976).

Shading lowers the digestibility of both leaf and stem tissue, associated with a lower total soluble carbohydrate and a higher lignin content in the shaded tissues (Wilson & Wong, 1982).

3.4 Prediction Of Digestibility

Edelsten & Corrall (1979) predicted sward digestibility from the time of the year (season effect), the length of time since the previous cut, and the weight of the harvested yield. In their opinion, by relating digestibility to the phenological stage of development of the canopy, their model could provide a more general basis with wider application

than their present model.

Though the prediction of forage digestibility from the stage of development of the canopy has been attempted in the case of legume forages (Kalu & Fick, 1981), this seems not to have been done for grasses. Digestibility of the latter has been predicted on a total-herbage basis from canopy age and heading-date (Green et al., 1971).

MATERIALS AND METHODS

4.1 Pot Experiments

Use was made of hybrid pennisetum cv. A23xN20 originating from the hybrid pennisetum nursery of the experimental farm of the Volcani Centre at Beit Dagan.

4.1.1 Exp. 1: The effect of tiller length on re-growth after defoliation

Rooted tillers, representing the entire range of tiller lengths of six-week old plants (4 to 42cm), were separated from pot-grown plants and placed in water during 2 days for promoting further root development. Thirty-six of the well-rooted tillers each were defoliated at 6 cm above the root crown and placed in 250 ml containers filled with vermiculite and regularly watered with a complete nutrient solution. After 14 days of undisturbed growth the re-growth of the tillers was recorded in terms of:

1. Tillers from which the apical meristem was not removed or damaged following defoliation, and continued to produce new leaves. These are referred to as "intact" tillers.

2. Tillers from which the stem apex was removed following defoliation of the main stem. These are referred to as "decapitated" tillers.

3. "New" tillers arising from basal buds (basal

tillers).

4.1.2 Exp. 2: The effect of the length of the pre-cutting period on plant structure and the re-growth of shoot

Ninety white-painted 15-liter plastic pots were filled with a mixture of gravel, vermiculite, and peat (40:40:20), respectively. They were placed in the open. Underneath each pot a piece of wood was placed to allow free drainage of excess water from the pot. The pots were placed at 1x1m between each other in a 9x10 rectangular grid.

Aerial tillers were separated by hand from mature stems of one plant and rooted in Jiffy pots filled with peat. Six well-rooted tillers were planted in each pot on June 10, 1985. Tillers which failed to take well were replaced on June 12.

The pots were watered three times a day through a drip-irrigation system, with one emitter (8 l. per hour) per pot. Irrigation was at first until excess water drained from the pots, but was later reduced when some leaf yellowing occurred, apparently caused by the poor aeration of the soil mixture. The irrigation water contained a complete fertilizer diluted to 200ppm N.

The pots were randomly assigned to one of three treatments, which were precutting periods of 2, 4, or 6 weeks (named PC2, PC4, and PC6, respectively). On Day 0 (July 27, 1983) all the plants were cut. Six pots of each precutting

treatment were chosen at random before cutting, and their canopy structure determined (as will be described later).

Subsequently, twice a week (every 3 or 4 days) for a period of 6 weeks (till August 27, 1983) two pots were selected at random from each precutting period and their canopy structure determined.

Canopy structure was characterized as follows:

1. The length of each tiller was measured from the cutting level to the top ligule (i.e. of the youngest fully expanded leaf).
2. They were then graded according to their length into length classes differing 3cm between each other: Class 1 from 0 to 3cm, class 2 from 3 to 6cm, ... class 14 from 39 to 42cm.
3. For each class the following was recorded: (a) Number of intact tillers (b) number of decapitated tillers (c) dry weight of leafblades (d) dry weight of stem+sheath and (e) apical distance. The latter was determined for each decapitated tiller by halving it longitudinally with a sharp knifeblade in order to detect the location of the stem apex. The distance measured between the stem apex and the top ligule is referred to as the apical distance. The total number of tillers and total weight per plant was calculated by summing the contents of the classes.

4.1.3 Exp. 3: The relationship between tiller length and digestibility

The experimental details are as for Exp. 1. Two, four, or six weeks after Day 0 one of the two pots harvested of each precutting treatment was selected. The dried contents of tiller classes 2, 4, 6, 8, and 10 (tiller lengths 3 to 6, 9 to 12, 15 to 18, 21 to 24, and 27 to 30cm, respectively) were ground coarsely, mixed well, and a representative sample was then ground finely in a coffee-grinder. This was analyzed for in vitro dry matter digestibility (IVDMD).

4.2 Field Experiments

Use was made of hybrid pennisetum cv. 23AxN23 originating from the hybrid pennisetum nursery of the experimental farm of the Volcani Institute at Beit Dagan.

4.2.1 Exp. 4: Parameter identification for the simulation model

Apical distance:

Tillers varying in length from 18 to 80 cm were selected at random in the field of a 5-wk-old well-developed canopy. They were cut 10cm above soil level and the length of each was measured from the cut surface to the top ligule (i.e. of the youngest fully-expanded leaf). Afterwards each

tiller was halved longitudinally in order to detect the location of the stem apex.

Tiller weight and length relationships:

Tillers varying in length from 6 to 110 cm were selected at random in the field when the canopy was 3 and 6 weeks old, respectively. Each tiller was cut at soil level and divided into 2 fractions: (a) the basal part measuring 10 cm long and (b) the remainder. Both fractions were dried at 70 °C in a forced-air oven until constant weight. The weight of the basal fraction is termed "residual tiller weight".

A second batch of tillers was similarly selected and divided into (a) leafblades and (b) stem+sheath.

4.2.2 Exp. 5 : The effect of cutting frequency on tiller production, dry matter accumulation, and canopy structure

In the summer of 1983 aerial tillers separated by hand from mature stems were planted in the field at the experimental farm of the Volcani Centre at Beit Dagan. The experiment was of a block design with 6 blocks (replicates) each measuring 12 x 12 m. Two treatments were imposed: cutting intervals of 3 weeks or of 6 weeks during a period of 130 days. Each plot measured 6 x 12 m. Plants were spaced at 60 x 60 cm, but approximately 15% of the plants did not survive the winter, so that the density was about 24,000 plants per ha.

The field was sprinkler-irrigated once a week at night at a rate of 7 mm day^{-1} (approximately 80% of the Class A pan evaporation rate). Former irrigation experiments with this grass in the same field showed that this amount amply meets its water requirements.

P (as superphosphate) and K (as potassium chloride) were applied at the start of the experiment (summer 1984) at the rate of 48 and 145 kg ha^{-1} , respectively. N (as ammonium sulphate) was added before each irrigation at 35 kg ha^{-1} and hand distributed.

The cutting treatments started on May 10, 1984 (with a cleaning cut of all plots) and terminated on September 17. During that period 6 cuttings were carried out at 3-wk intervals (31/5, 25/6, 16/7, 6/8, 27/8, 17/9), and 3 cuttings at 6-wk intervals (25/6, 6/8, 17/9).

Every 10 days one plant randomly chosen was harvested from each plot, weighed green, and the total number of tillers counted. Approximately one-third was taken for determining the percentage of dry matter. The remaining two-thirds were used to determine the canopy structure as follows:

1. The length of each tiller was measured from the cutting level to the top ligule (i.e. the youngest fully expanded leaf).
2. They were then graded according to their length into up to 16 tiller classes, differing 5cm in length between each other: Class 1 from 0 to 5cm long, class 2 from 5 to 10cm, ...class 10 from 45 to 50cm long. Above 50cm the classes

differed 10 cm in length between each other: Class 11 from 50 to 60cm, class 12 from 60 to 70cm, ...class 16 from 100 to 110cm long. The number of tillers in each class was counted.

All the tillers of an identical class from the six replicates per treatment were merged. From each class a manageable sample, depending on the size of the tillers, was taken to determine parameters that relate to their re-growth capability after cutting and to their digestibility: (a) Number of intact tillers, (b) number of decapitated tillers, (c) number of dead tillers, i.e. those of which the youngest leaf is dead, which indicates the lack of apical acitivity (Langer, 1956) (d) dry weight of leafblades and (e) dry weight of stem+sheath.

The difference between the total number of tillers and the number of "dead" tillers is termed the number of "live" tillers, and is used for comparison with the simulated tiller number, which consists of live tillers only.

In order to simplify the presentation of canopy structure data, the tiller classes were grouped into four size groups: less than 10cm long, from 10 to 20cm, from 20 to 40cm, and longer than 40cm.

4.2.3 Exp. 6: The relationship between canopy structure and digestibility

The experimental details are those reported for Exp. 4. The following samples were taken for determining the in vitro

dry matter digestibility:

1. From the 6-wk cutting intervals only, when the canopy was 21, 31, and 42 days old.

3. For tiller classes 2, 4, 6, 10, and 12 only (tiller lengths 5 to 10cm, 15 to 20, 25 to 30cm, 45 to 50cm, and 60 to 70cm respectively), leafblades and stem+sheath separately.

4.2.4 In vitro digestibility determination

The in vitro digestibility determination (IVDMD) was carried out according to the Tilley & Terrey (1962) two-stage technique.

RESULTS

5.1 The Effect Of The Length Of The Precutting Period On Plant Structure And The Re-growth Of Shoot.

The length of the precutting period hardly affected the morphology of the tillers on Day 0 (Exp. 2; Fig. 2-4). The weight of a tiller (W) was found to be exponentially related to its length (L):

$$\ln(W) = -3.865 + 1.815 \times \ln(L) \quad (r^2 = 0.97, n = 30) \text{ (Fig. 2)}$$

Also, the leafblade weight per tiller (LB) was found to be exponentially related to the whole-tiller weight (W):

$$\ln(LB) = -0.283 + 0.935 \times \ln(W) \quad (r^2 = 0.99, n = 30) \text{ (Fig. 3)}$$

Whether a tiller was decapitated or not at defoliation depended upon its length - the longer the tiller, the greater the chance of decapitation (Fig. 4). However, there was a relatively narrow range of tiller lengths where the percentage of decapitated tillers moved from 0 to 100%. Fifty percent of decapitation occurred at approximately 12 ± 0.3 cm (mean $\pm$ SE) with only slight differences between the treatments.

This distance was related to the location of the stem apex, which was found to be about 12 cm below the top ligule, regardless of tiller length, however slightly shorter for

Fig. 2: The effect of the length of the precutting period on the tiller weight/tiller length relationship of pot-grown hybrid pennisetum (Exp. 2).

Fig. 3: The effect of the length of the precutting period on the leafblade weight/whole tiller weight relationship of pot-grown hybrid pennisetum (Exp. 2).

Fig. 4: The effect of tiller length and the length of the precutting period on tiller decapitation of pot-grown hybrid pennisetum (Exp. 2). Means of 6 replicates. (Standard errors indicated as vertical bars).

Table 1: Number of tillers per pot of hybrid pennisetum plants following precutting periods of 2, 4 or 6 weeks. Means of 6 pots, 6 plants per pot (Exp. 2).

Treatment	Precutting period (weeks)	Tiller length (cm)				Intact	Decapitated	Total
		<6	6-12	12-24	>24			
PC2	2	61(48)*	54(43)	10(8)	1(1)	111(88)	15(12)	126
PC4	4	40(26)	67(44)	42(27)	5(3)	114(75)	39(25)	154
PC6	6	12(14)	23(27)	36(43)	13(16)	42(50)	42(50)	84

* Percentage of total

PC2. This may explain why the fifty percent of tiller decapitation occurred at a slightly shorter tiller length for PC2 than the other precutting treatments.

While the length of the precutting period hardly affected the morphology of the individual tiller, it did greatly influence the plant structure at the day of cutting (Table 1). Differences in plant structure between the precutting treatments at the day of cutting can therefore not be attributed to changes in tiller morphology.

The increase in the length of the precutting period caused an increase in the number of tiller classes and a decrease in the relative number of small tillers. Also the total number of tillers per pot at Day 0 was affected (Table 1). The pots of PC6 had the lowest total tiller number per pot, while those of PC4 had the highest. Because of the different canopy structure the ratio of intact to decapitated tillers per pot also varied between the precutting treatments, PC2 consisting mainly of vegetative (intact) tillers, while in PC6 about half of the tillers were culmed and had been decapitated at defoliation.

Following defoliation the re-growth of the plants in terms of dry matter accumulation was similar irrespective of precutting treatment (Fig. 5A). Though the dry weight accumulation was similar, tiller number per pot differed greatly between the treatments (Fig. 5B). PC2, which had the highest tiller number on Day 0, attained the lowest tiller number in the re-growth, while PC6 attained the highest tiller number. In all treatments the maximum tiller number

Fig. 5A:

$$Y(2) = -11.4 + 6.32 \times \text{Day} - 0.0427 \times \text{Day}^2 + 0.00237 \times \text{Day}^3 \quad (R^2 = 0.98, n = 10)$$

$$Y(4) = -67.9 + 20.5 \times \text{Day} - 0.795 \times \text{Day}^2 + 0.0141 \times \text{Day}^3 \quad (R^2 = 0.96, n = 10)$$

$$Y(6) = -66.0 + 18.1 \times \text{Day} - 0.691 \times \text{Day}^2 + 0.0132 \times \text{Day}^3 \quad (R^2 = 0.98, n = 11)$$

Fig. 5B:

$$Y(2) = 129 + 3.08 \times \text{Day} - 0.0557 \times \text{Day}^2 + 0.000133 \times \text{Day}^3 \quad (R^2 = 0.29, n = 10)$$

$$Y(4) = 42.0 + 15.2 \times \text{Day} - 0.441 \times \text{Day}^2 + 0.00373 \times \text{Day}^3 \quad (R^2 = 0.90, n = 10)$$

$$Y(6) = -77.8 + 33.6 \times \text{Day} - 1.15 \times \text{Day}^2 + 0.0125 \times \text{Day}^3 \quad (R^2 = 0.97, n = 11)$$

Fig. 5C:

$$Y(2) = -3.69 + 1.01 \times \text{Day} - 0.0397 \times \text{Day}^2 + 0.00098 \times \text{Day}^3 \quad (R^2 = 0.88, n = 11)$$

$$Y(4) = -6.40 + 2.15 \times \text{Day} - 0.106 \times \text{Day}^2 + 0.0020 \times \text{Day}^3 \quad (R^2 = 0.98, n = 10)$$

$$Y(6) = -3.713 + 2.12 \times \text{Day} - 0.135 \times \text{Day}^2 + 0.0026 \times \text{Day}^3 \quad (R^2 = 0.89, n = 11)$$

Fig. 5: The effect of the length of the precutting period on a) dry weight accumulation b) total number of tillers and c) percent of decapitated tillers of pot-grown hybrid pennisetum (Exp. 2).

was attained at about 3 weeks after defoliation, with a slight decrease toward the end of the growth period, due probably to tiller death and decomposition.

The percent of decapitated tillers per pot during re-growth reflects the relative size-distribution of the tillers: The lower the average tiller weight, the shorter the average tiller length, and thus the lower the proportion of decapitated tillers. Thus, PC6, with a high tiller number but similar dry weight accumulation as PC2 and PC4, thus showed a lower proportion of decapitated (i.e. elongated) tillers during most of the course of re-growth (Fig. 5C). The presence of decapitated tillers immediately following defoliation in this treatment was due to the warped re-growth of several tillers which had been cut closely above the stem apex. They usually died subsequently.

5.2 Parameter Identification For The Simulation Model SIMPIL

SIMPIL was developed to simulate the course of dry matter production of a hybrid pennisetum canopy from the simultaneous changes in number and weight of its tillers. It is based on concepts developed in a model named TILDYN which was validated with Rhodes grass (Dayan et. al., 1981). The program is written in Basic-Plus of the DIGITAL PDP-11 (Appendix 1 and 2).

Tiller classes

The total number of tillers in the canopy was divided into length classes - each 5 or 10cm long defined as a separate class (see 4.2.2) - representing different developmental stages. Tiller length was chosen as a classifying parameter.

Tiller growth and development, however, proceeded on the basis of tiller weight. A close relationship was found between the tiller weight (W) and its length (L), from which the specific average and maximum weight was determined for each tiller class:

$$\ln(W) = -5.70 + 1.96 \times \ln(L) \quad (r^2=0.95, n=34) \quad (\text{Exp. 4})$$

If, as a result of tiller growth, the mean weight of the tillers in a particular class exceeded the specified average weight, a quarter of the tillers (the heaviest) were moved to the next higher class. If it exceeded the specified maximum weight, the entire number of tillers was transferred to the next higher class according to the "boxcartrain" procedure of De Wit & Goudriaan (1978).

Tiller re-growth

Tiller re-growth is first and foremost dependent on whether its apical meristem is removed (or damaged) with cutting. This is considered a function of three parameters: The length of the tiller, the apical distance, and the height of defoliation. The apical meristem of the field grown tillers was located at an almost constant 19.3 ± 0.4 cm

measured from the top ligule (Exp. 4). Whether the difference between the apical distance which was found to be approximately 12cm in pot-grown plants (Exp. 2) and that of the tillers from the field experiment is the result of the cultivar difference or of the different growing conditions could not be ascertained. A tiller is decapitated upon cutting if its length is greater than the sum of the apical distance plus the cutting height.

Since in our field experiment (Exp. 5) the cutting height was approximately 10 cm above the soil surface and the apical distance was approximately 20 cm, any tiller taller than 30 cm is considered to be decapitated following defoliation. However, extensive observations of tillers growing in pots and in the field showed that tillers which were not decapitated but defoliated adjacent to the apical meristem were also not capable to continue leaf extension. This lack of re-growth was probably due to the exposure of the apical meristem following the loss of the protective leaves and sheaths. Thus tillers from 25 to 30 cm tall are also considered to be decapitated as a result of defoliation.

Intact tillers initiate their re-growth from the residual tiller material. The regression of residual tiller weight (RW) on total tiller weight (W) was:

$$\ln(RW) = -0.34 + 0.634 \times \ln(W) \quad (r^2=0.96, n=33) \quad (\text{Exp. 4})$$

Tillers which stem apex was removed at defoliation are

dependent for re-growth on the development of basal buds into new tillers. The average number of basal buds per decapitated tiller producing new tillers was found to be 3.6 ± 0.2 (Exp. 1), irrespective of the length of the main stem. New tillers did not appear instantaneously, but gradually over a period of approximately 10-14 days. In the model, the total number of decapitated tillers is multiplied by 3.5 to obtain the total number of potential basal tillers (i.e. the total number of basal buds). The first day following defoliation a fraction ($1/5$) of these basal buds are transferred into the smallest tiller class, where they start with an initial weight of 0.02 g per tiller (an estimate). Each subsequent day the same fraction of the remaining basal buds is similarly transferred. At Day 10 following defoliation 90% of the buds have "developed" into tillers.

Tiller growth

The growth of tillers is considered to depend on the average daily temperature, the total daily radiation received, and on the weight of the photosynthetic tissue, assuming water and minerals are not limiting growth. All tillers in a given class contribute the same growth rate. For each day the average daily temperature is taken from current readings and the total daily radiation from long term averages. Tillers in the tallest class receive full light while the shorter tillers receive proportionally less light depending on the cumulative leaf area index and on the extinction coefficient calculated according to the formula of

Monsi & Saeki (1953). The extinction coefficient used equals 0.5, an average value from different grasses (Begg et al., 1964; Brown & Blaser, 1968).

From the average daily temperature and radiation reaching each tiller, its relative growth rate (RGR) is calculated using an equation experimentally derived for hybrid pennisetum by Muldoon (1979). This is multiplied by the weight of the photosynthetic tissue (leaf blades and sheaths only) in order to obtain the daily growth increment. The relationship of leaf-blade weight (LW) on whole tiller weight (W) was experimentally determined and is characterized by a quadratic regression:

$$\ln(LW) = -0.22 + 0.85 \times \ln(W) - 0.023 \times (\ln(W))^2 \quad (R^2=0.99, n=98) \\ (\text{Exp. 4})$$

The weight of sheaths was estimated to be equal to 20% of the leaf blade weight.

The leaf area per tiller is calculated by multiplying the leaf weight times the specific leaf area (SLA) which was determined experimentally. SLA decreases as the tiller increases in length. The leaf area is summed for all the tillers in each class to obtain the partial leaf area index for each class separately. The irradiance reaching any one particular class is determined by summing the partial leaf area indices of all the tiller classes taller than itself and substituting the value obtained (the cumulative leaf area index) into the light extinction formula.

As the weight of the canopy increases, the amount of light reaching the lower tiller classes decreases, and consequently the RGR as well. When the calculated RGR is less than $0.02 \text{ g g}^{-1}\text{day}^{-1}$ (an estimate) tiller death is assumed to occur. This is achieved by removing a tenth (an estimate) of the tiller number (and weight) of each class for which the RGR reaches this value.

Lateral tillering

In addition to tillers initiated from basal buds following defoliation, new tillers are produced as a result of lateral tillering. It was found that only those tillers between 10 and 20 cm long produce lateral tillers. Those shorter did not yet reach the minimal size required, while those taller started internode elongation which causes depression of lateral tiller production most probably due to apical dominance (Jewiss, 1972).

The rate of lateral tiller production is limited by the rate of leaf production which in turn is determined by temperature (Muldoon & Pearson, 1979a). It is assumed that for each leaf one lateral tiller is produced with an estimated initial weight of 0.02 g.

Production of lateral tillers, as the development of basal buds, is halted when the RGR is below the value required for their maintenance ($0.02 \text{ g g}^{-1}\text{day}^{-1}$).

Defoliation

Part of each tiller remains as stubble on the field as

the residual tiller weight. The yield is the sum of the forage removed from all the tillers in the canopy upon cutting.

5.3 Measured And Simulated Effect Of Cutting Frequency On Tiller Production, Dry Matter Accumulation And Canopy Structure.

The course of dry matter accumulation after cutting generally started with an initial period of slow re-growth followed by a period of quick linear growth (Fig. 6A,C). However, the rate of initial re-growth after 6 weeks of growth was almost 4 times slower than after 3 weeks of growth. On the other hand the rate of quick linear growth was quite similar for both cutting cycles. There was good agreement between the courses of measured and simulated dry matter accumulation.

The increase in number of tillers during the 3 weeks of growth usually proceeded at a uniform rate, however the simulated tiller production generally overestimated the measured tiller production (Fig. 6B). In the 6-wk treatment the number of tillers at Day 10 was approximately 6 times less than in the 3-weeks treatment. During the 6-wk period of growth the measured number of tillers was similar to the simulated number of tillers (Fig. 6D). Furthermore it should be noted that during the 6-wk period of growth a decrease in the total number of tillers occurred (which started around

Fig. 6: Measured and simulated dry matter accumulation and tiller number of hybrid pennisetum under 3-wk and 6-wk cutting frequencies (Exp. 5).

Day 25) with a net result of the loss of approximately 40% of the tillers, which apparently died because of the lack of light required for their development.

As expected, the distribution of tiller lengths after 3 weeks was very different from the 6 weeks of re-growth (Table 2). At the end of the 3-wk period more than 90% of the tillers were less than 20 cm long (above cutting height), most of them intact. Contrarily, after 6 wks of growth almost 70% of the tillers were longer than 20 cm and thus were

Table 2: Measured and simulated number of tillers, weight per tiller, percentage decapitated and dead tillers of different length classes at the end of the cutting interval. Means of six 3-week and three 6-week intervals (Exp. 5).

	Tiller length (cm)							
	<10	10-20	20-40	>40	<10	10-20	20-40	>40
	Cutting intervals							
No. tillers per m ²	3 weeks				6 weeks			
Measured	177(63)*	83(29)	23(8)	-	24(15)	28(17)	51(31)	61(37)
Simulated	148(50)	88(30)	58(20)	-	29(19)	27(17)	53(34)	47(30)
Weight per tiller (g)	0.16	1.69	2.93	-	0.53	1.30	3.48	7.73
Decapitated tillers (%)	0	15	91	-	0	0	78	100
Dead tillers (%)	3	0	0	-	70	48	1	0

* Percentage of total

mostly decapitated upon defoliation. Additionally a high proportion of dead small tillers was found.

The average measured and simulated dry matter yields of the 3-wk cutting frequency were 423($\pm$ 55) and 375 g m⁻², and of the 6-wk cutting frequency were 801 ($\pm$ 171) and 821 g m⁻² respectively. Since climatic conditions during the season were quite uniform only small differences were found between yields obtained after cutting at identical intervals.

A significant finding is that the total dry matter yield of 2 cuttings of 3-wk cycles each, was similar to the yield obtained after one cycle of 6 weeks.

5.4 The Relationship Between Canopy Structure And Digestibility.

Pot Experiment (Exp. 3):

Between Day 14 and Day 42 the size of tillers increased (Table 3). The digestibility of the tillers when compared at each of the cutting dates was similar irrespective of tiller length; however, between Day 14 and Day 42 the digestibility of the whole-herbage decreased by approximately 10% units.

Table 3: The effect of plant age and of tiller length on in vitro digestibility (%) of pot-grown hybrid pennisetum (Exp. 2). SD=0.4.

Plant age (days)	Tiller length (cm)					
	3-6	9-12	15-18	21-24	27-30	Mean
	Precutting period					
	2 Weeks (PC2)					
14	78.7	76.1	-	-	-	77.4
28	74.9	73.9	75.1	-	-	74.6
42	71.2	72.7	71.3	69.3	70.2	70.9
	4 Weeks (PC4)					
14	78.7	80.4	-	-	-	79.6
28	75.4	72.2	71.7	-	-	73.1
42	70.2	68.8	69.7	68.6	67.7	69.0
	6 Weeks (PC6)					
14	82.4	80.7	-	-	-	81.6
28	76.1	75.6	74.6	-	-	75.4
42	69.4	69.7	69.8	68.5	68.0	69.1

There was a significant effect of the length of the precutting period on digestibility. PC6 was of a higher digestibility than PC2 and PC4 on Day 14 and on Day 28, but on Day 42 they were of similar digestibility.

Field Experiment (Exp. 6):

No significant effect on digestibility was attributed to differences between the three 6-week cutting cycles, and therefore the results are presented as means (Table 4).

The results from the whole tiller digestibility (weighted for the relative proportion of leaf and stem weight) were similar to those of the pot experiment, i.e. the digestibility of the tillers decreased with time, regardless of tiller length.

However, though tiller length was not related to whole tiller digestibility, it was related to the digestibility of both leafblades and stem, when considered separately. In the case of leafblades the digestibility increased with tiller length, while that of the stem decreased with tiller length. The two opposed tendencies however, compensated each other.

The digestibility of leafblades was generally higher than of stems, except for the smaller tillers on Day 42.

Table 4: The effect of canopy age and of tiller length on the digestibility of stems, leafblades, and whole tillers (weighted for leafblade/stem ratio) of field-grown hybrid pennisetum (Exp. 5).

Means of 3 cutting cycles of 6 weeks each. SE=1.1.

Age (days)	Tiller length (cm)					
	5-10	15-20	25-30	45-50	60-70	Mean
	Stem digestibility (%)					
21	70.9	68.7	-	-	-	69.8
31	66.5	64.9	66.5	-	-	68.0
42	63.8	62.1	60.9	59.3	58.6	60.9
	Leaf digestibility (%)					
21	74.7	68.4	-	-	-	71.3
31	65.5	68.1	70.8	-	-	68.1
42	58.0	59.5	62.6	63.6	65.1	61.8
	Whole-tiller digestibility (%)					
21	73.3	68.5	-	-	-	70.9
31	64.2	67.2	69.2	-	-	66.9
42	59.0	60.2	62.0	61.6	61.6	60.9

DISCUSSION

6.1 Tiller Morphology

The weight of a tiller increased exponentially with its length (Fig. 2). Both leafblade weight (Fig. 3) and residual tiller weight increased with tiller weight. The simplicity of these relationships, and the fact that they were little affected by cutting treatment, made them very suitable for use in the simulation program. The relationship between tiller length and tiller weight also enabled the use of a tiller classification with classes defined simultaneously by weight as well as by length. In this way it was possible to compare the predicted canopy structure with the measured canopy structure where classes were defined by length (Table 2).

A finding of considerable importance was that the stem apex of the elongating tiller was located at a constant distance below the top ligule irrespective of tiller length. In the pot experiment the apical distance measured 12cm (Fig. 4), in the field it was 20cm long (Exp. 4, 5.2), while Muldoon & Pearson (1977) reported a length of 16cm. These differences of apical distance are possibly caused by differences in the variety used and also in growing conditions.

The constant length of the apical distance provides a sound prediction of whether a tiller will be decapitated following defoliation. A tiller is decapitated when its

length is greater than the sum of the apical distance and the cutting height (Fig. 1). Thus when the canopy structure (as measured in terms of tiller length distribution) is known, the proportion or the number of decapitated tillers can be predicted. No reports in the literature were encountered concerning a similar predictive use of the apical distance.

Rechentín (1956) observed that elongated tillers of different grass species vary in the number of basal nodes. We found that elongated tillers of hybrid pennisetum have between 3-4 basal nodes per tiller. Each basal node carried one bud (basal bud) which was dormant during stem elongation, but upon defoliation of the tiller they quickly resumed growth. This differs from the hybrid's female parent, pearl millet, whose basal buds grow only with difficulty following defoliation (Begg, 1956). However, the length of time that a bud is inhibited seems to adversely affect the capability of the bud to develop once it is released from inhibition (Mitchell, 1953).

6.2 Effect Of Length Of Growth Period On Canopy Structure

Considering at first the effect of the length of growth period on the total tiller number, it was found that following defoliation tiller number rapidly increased asymptotically till it reached a maximum value (Fig. 5B; Fig. 6B,D). This rapid increase is associated with the quick re-growth of intact tillers and the simultaneous growth of

basal buds (Muldoon & Pearson, 1979b).

After about 3 weeks following defoliation no new tillers were produced. Whether the halt in tiller production was due to elongation of the tillers (Jewiss, 1972) or to the effect of shading (Langer et al., 1964), or both, is not clear. However, since production ceased after similar periods of time in both the pot and the field experiment, and under different cutting treatments, it seems more likely to be due to the effect of stem elongation, which is probably less affected by growing conditions and cutting treatments than the amount of light received at the base of the plant.

Following the attainment of maximum tiller number, the number of tillers remained constant or slowly decreased due to the death and decomposition of the smallest tillers (Fig. 5B; Fig. 6B,D). A similar decline in tiller number was reported for this grass by Muldoon & Pearson (1977), for Napier grass (Ferraris & Sinclair, 1980b), and for sugarcane (Shih & Gascho, 1980).

With time the number of elongated tillers (i.e. tillers that were decapitated when the plants were defoliated) increased, the result of the growth which is associated with the increase in length of the individual tillers (Table 1; Table 2). The proportion of elongated tillers of the total number of tillers remained relatively constant as long as new tillers were produced. However, following the halt in tiller production the proportion of elongated tillers rapidly increased (Fig. 5C). Contrarily the proportion (and actual number) of vegetative tillers rapidly declined following the

halt in tiller production.

A great proportion of the vegetative tillers were found to be dead by the end of six weeks of growth (Table 2). A dead tiller may for a while contribute to the weight of the canopy, until it is decomposed, but it does not contribute to the growth of the canopy nor to the re-growth following defoliation. The occurrence of tiller death seems to be related to the competition between the tillers for limiting resources (Aikman & Watkinson, 1980). In our experiments where water and minerals were supplied liberally, probably light was the limiting factor. Tiller death was most frequent among the smallest tillers, probably because tiller length determines the ability to gain access to the light (Ludlow, 1978) and because the taller tillers support the smaller tillers with assimilates only at a very young stage of growth (Ong et al., 1978; Quinlan & Sagar, 1962).

6.3 Effect Of Canopy Structure On Tiller Number and Dry Matter Accumulation Following Defoliation

The plants in the pots which grew 2 weeks only before cutting were completely vegetative (Table 1). Following defoliation most of the tillers re-grew, so that at the first sampling after 4 days of re-growth the number of tillers was similar to that at defoliation (Fig. 5B). There was only a slight increase in tiller number during the remaining growth

period ($R^2=0.29$).

On the other hand, following a 6-wk precutting period approximately half of the tillers were decapitated at defoliation, in addition to the fact that overall tiller number was very low in comparison to the other precutting treatments of 2 and 4 weeks. Following defoliation very few tillers re-grew; however, tiller number rapidly increased during the first 3 weeks of re-growth due to the initiation of tillers from basal buds. Ten days following defoliation tiller number was higher following a 6-wk precutting period than following a 2-wk precutting period.

These results emphasize the importance of the presence of vegetative tillers for quick and immediate re-growth, and illustrate the ability of the grass plant to re-grow by different means, that is, by intact tillers on the one hand or by basal buds on the other. The importance of axillary tillering in tiller production was not investigated, but seems not to have been of major importance.

Following the 4-wk precutting period the plants had both a high number of intact tillers as in the the 2-wk precutting treatment, as well as a high number of decapitated tillers similar to the plants of the 6-wk precutting period (Table 1). It might have been expected that following defoliation this treatment should exhibit during its re-growth a tiller number higher than that of both of the two other precutting treatments. Instead tiller number was intermediate between the other two treatments; most of the intact tillers seemed to re-grow, but the number of basal tillers that developed

was much lower than expected.

The lower than expected number of basal buds that developed following the 4-wk precutting period might be the result of an inhibiting effect of the re-growing tillers on the basal buds; Fast re-growth of intact tillers makes a larger demand on reserve substances (proteins and carbohydrates) in the remaining stem weight than the slow re-growth of the basal buds (Muldoon & Pearson, 1979). The competing demands of intact tillers and basal buds might have led to the suppression of the basal buds.

Following the 6-wk precutting period in the pot-grown plants the percentage of elongated (=decapitated) tillers was much lower than the other two treatments during most of the re-growth period (Fig. 5C). This is the result of the fact that the re-growth following the 6-wk precutting period consisted mostly of newly initiated tillers from basal buds, while in the other treatments most of the re-growth consisted of re-growing (vegetative) tillers. The tillers that developed following defoliation were therefore physiologically less developed following the 6-wk precutting period than following the shorter precutting periods.

The results of the field experiment (Fig. 6B,D) were similar to those of the pot experiment. The canopy at the end of the 6-wk cutting interval consisted of relatively few vegetative tillers (taking into account tiller death), and during re-growth tiller number lagged for a considerable period of time until the basal tillers had developed, in comparison to an immediate and quick re-growth of tillers

following the 3-wk cutting interval.

In the field experiment (Fig. 6A,C) the dry matter accumulation of the 6-wk intervals lagged considerably behind that of the 3-wk intervals. This was due to the higher rate of tiller production immediately following defoliation of the 3-wk intervals (Ferraris & Sinclair 1980; Zarroug et al., 1983), the result of the fast re-growth of the intact tillers. In the pot experiment, on the other hand, the tiller number following the 2-wk precutting period was higher than that following the 6-wk precutting period for only a limited period of time, after which it was exceeded by the 6-wk precutting treatment, leading to small differences only in dry matter accumulation.

In spite of the fact that the number of harvests made at the 3-wk cutting intervals was twice that of the 6-wk cutting intervals, the total yields obtained from both intervals during 18 weeks of growth was similar. Since the rate of dry matter accumulation during the linear phase of growth was not affected by cutting treatment, it means that both cutting treatments had similar proportions of growth in the exponential and in the linear phase; that is, the proportion of time of the entire season that the canopy was in the exponential phase relative to the linear phase was similar under both cutting frequencies. With the number of harvests doubled, the length of the exponential phase of the 3-wk cutting frequency was obviously half that of the 6-wk cutting frequency.

6.4 Simulation Of The Effect Of Cutting Frequency On Tiller Production, Dry Matter Accumulation And Canopy Structure

On the day of the start of the field experiment (Exp. 5), the canopy structure was quantitatively characterized and used as an initial setting for the simulation. Subsequently the predicted canopy structure at the end of the first cutting interval was used as an initial setting for the simulation of the second cutting interval, and so forth. This means that inaccurate prediction of the canopy structure at the end of the cutting interval will adversely affect the results from simulation of the succeeding cutting intervals. This puts considerable emphasis on the effort to obtain accurate information on the structure of the canopy at the beginning of the simulation period.

Due to the presence of mostly vegetative tillers at the start of the experiment the growth of the first cutting interval was quick, and thus the growth of the first 6-wk cutting interval did not exhibit the typical lag in dry matter production of the next two cutting intervals (Fig. 6C).

The simulated canopy structures at the end of the cutting intervals were similar to the measured ones (Table 2). This similarity was dependent on the accurate simulation of the tiller dynamics of the canopy, that is, simulation of the changes in tiller number and of the differential growth rates of tillers varying in size and in location in the

canopy.

The predicted tiller number following defoliation was greatly affected by the simulated canopy structure (Fig. 6B,D). Following the 6-wk interval was a marked lag in the number of tillers produced compared with the re-growth after the 3-wk interval. The simulated rates of tiller production differed between the cutting frequencies, because they depended on different means of tiller production; The model predicted a high percentage of the tillers of the 3-wk interval to re-grow, whereas in the 6-wk intervals mainly basal tillers developed.

Under the 3-wk cutting frequency the simulated tiller production was much higher than measured. The reason for this is uncertain, but part of the reason might lie in the overestimated number of basal tillers that develop. The simulated canopy structure following a 3-wk interval includes an appreciable number of decapitated tillers, higher than the measured number (Table 2). This would give rise to the development of a high number of basal tillers, while it was observed in the pot experiment that the re-growth of intact tillers seemed to inhibit the development of basal buds. The model, however, neglects the effect of re-growing tillers on basal bud development.

The lag in tiller number following the 6-wk as compared with the 3-wk cutting interval resulted in a lag in dry matter accumulation, and extended the exponential growth phase in the first. However, the maximum predicted rate of dry matter accumulation was not affected by the length of the

cutting interval. This rate was approximately $300\text{kg ha}^{-1}\text{day}^{-1}$, similar to that predicted by Dayan et al. (1981) for Rhodes grass which was growing in the same location. Due to the longer exponential phase predicted for the 6-wk cutting intervals, the overall predicted seasonal yield was similar for both cutting frequencies.

The simulated decrease in tiller number due to death closely approached the measured tiller number. The simulation of tiller death was of great importance for the prediction of the lag in re-growth of the 6-wk cutting frequency.

6.5 Evaluation of the SIMPIL model

In general it was found that the model successfully predicted the effect of cutting frequency on re-growth of hybrid pennisetum. Firstly this was achieved by simulating the tiller dynamics of the closed canopy so as to calculate the proper canopy structure at the end of the cutting interval, and secondly by simulating the effect of the canopy structure on the initial re-growth.

The possibility to use the model to predict the structure of the canopy throughout the growth period in terms of the tiller-length distribution, which is easily measured in the field, enables analysis of the tiller dynamics of the canopy and the interactions between tillers. Deviations of the actual from the measured canopy structure help pinpoint weaknesses in the model's mechanics or assumptions, which in

turn make it possible to seek improvements.

The model is relatively simple and mainly of a descriptive character. Most of the parameters describe morphological traits and are easily adapted for grasses different from hybrid pennisetum. Tiller growth was assumed to depend on leaf weight, radiation, and temperature. The model neglected, however, the influence of daylength, the diurnal temperature differences, the change in light quality whilst penetrating into the canopy, and temperature differences within the canopy.

The concept of light penetration into the canopy according to tiller classes was of major importance for simulating the preferential access of taller tillers to the incident radiation on the one hand, and for reducing the number of the smaller tillers through tiller death on the other hand. This concept, however, assumed that there is no effect of the smaller tiller classes on the interception of light by the tiller classes taller than itself.

A weakness of the model is that it does not take into account the mutual shading of tillers in the same class. Thus the growth increment for any class depends linearly upon the amount of leaf weight present, and can therefore theoretically exceed the maximum crop growth rate feasible under the given radiation and temperature conditions. Preventing this from occurring depends on a relatively large number of tiller classes, with relatively few tillers per class.

When the relative growth rate calculated for any class

fell below a critical value ($0.02\text{g}^{-1}\text{g}^{-1}\text{day}^{-1}$), tiller death was assumed to occur, at a rate of 10% of the tillers of that class each day. However, although the tiller is dead, it still contributes weight to the canopy. Eventually the tiller will decompose, a process taking more time the larger the tiller. However, this discrepancy in time between the death of a tiller and its disappearance in terms of its weight was ignored by the model, in simply detracting the tiller's weight from the tiller class at the same time of it's death. This inaccuracy probably had little effect on the predicted dry matter accumulation in the present evaluation experiment, because tiller death was limited to the tillers of low average weight. If tiller death would occur also in the taller classes, for example under cutting intervals longer than 6 weeks, this inaccuracy could become significant.

Tiller re-growth following defoliation was assumed to depend on morphological characteristics only, that is the residual tiller weight of the intact tiller, and the number of basal buds which develop from the decapitated tiller. Thus the possible effects of microclimatological changes, changes in the shoot/root ratio, or carbohydrate reserves were not taken into account. Also Dayan et al. (1981) disregarded the possible effect of these factors in simulating the re-growth of Rhodes grass. Whether these factors are of negligible importance and therefore can be disregarded requires further investigation.

The model assumes that stem elongation is a natural

consequence of the dry matter accumulation of the tiller. With the increase of weight the length of the tiller increases, and when taller than the apical distance (20cm) it is considered to be in the course of stem-elongation. As soon as the tiller elongates it stops producing axillary tillers. In reality, however, the process seems to be reversed. According to Smith & Rogan (1980), the dry matter accumulation of the parent tiller is inhibited by initiating axillary tillers, so that the parent tiller tends to remain of a rather constant size as long as it is initiating axillary tillers. It is only after the parent tiller is induced to elongate through an internal or external mechanism which is not yet fully understood, that it stops producing axillary tillers (Jewiss, 1972), and resumes the increase in weight (Smith & Rogan, 1980). However, since too little is known concerning the factors that induce stem elongation, a more realistic approach could not be implemented.

All in all the model in its present form predicted fairly accurately the effect of different cutting schedules on the re-growth of hybrid pennisetum, through the use of a relatively small number of simple-to-measure parameters. In this respect it served its purpose well and enhanced the understanding of the interrelationship between factors involved in the growth and re-growth after cutting of a grass canopy. It may be used to develop cutting strategies for the obtaining of maximum dry matter yield during the season.

6.6 The Relationship Between Plant Structure And Tiller Digestibility

The digestibility of leafblades decreases with the level of insert and age (Deinum 1976; Wilson 1976). The digestibility of the total leafblade mass of a young tiller should therefore be relatively high, because its leafblades are both of low insert as well as having aged little. In contrast, the total leafblade mass of a more mature tiller should be relatively low, the youngest leafblades being of high insert, while the leafblades of low insert have aged. Using tiller length as a measure of development, the leafblade mass of a tall tiller would be expected to be of lower digestibility than that of a short tiller.

Also the digestibility of the stem of a tall tiller should be lower than that of a short tiller. This is due mainly to the increasing lignification of the upper internodes (Pritchard et al., 1963).

Thus, when the development of a tiller is followed in the course of its growth from a young, short tiller, to a mature, tall tiller, a continuous decrease in digestibility of the whole tiller is expected. If a relationship between the digestibility of a tiller and its length could be established it was deemed feasible to predict the canopy digestibility from its component tiller population, if the tiller-length distribution was known.

The results of the digestibility tests (Table 3; Table

4), however, showed that at any one date digestibility of the different tiller classes was similar, regardless of tiller length. Instead, with the ageing of the canopy the digestibility of tillers of all the classes decreased. Explaining the discrepancy between these results, and the above hypothesis that a tiller decreases in digestibility with length, requires an understanding of what we call the "tiller dynamics" in a canopy.

Tiller dynamics refers to the change in number and age class^{of} the tillers in a developing canopy or plant. Two basic assumptions are made:

1. The tallest tillers at any one day were also the tallest tillers at any previous day and will also form the tallest tillers at any future day.
2. A tiller either remains constant or increases in size. It may die and decompose, but it does not decrease in size.

Allowing for these assumptions, the results of the whole-tiller digestibility will be analyzed. At first the results of the field experiment (Exp. 6) will be considered, where the plants were growing in a canopy.

Following the course of growth of the tallest tillers, from Day 21 to Day 42, it can be seen that their digestibility decreased from approximately 69 to 62% (Table 4). Thus, during the development of a tiller its digestibility decreases, which is what was expected.

However, not all the tillers grew simultaneously at the same rate in the canopy. It is seen (Table 4) that small tillers (5-10cm) were present at each of the cutting dates.

New tillers appeared only up to around Day 21 (Fig. 6D), so that it can be deduced that the smallest tillers present on Day 42 were those present on Day 31, and in all likelihood also derived from those present on Day 21. When the digestibility of these tillers was analyzed, it was found that it decreased by about 14% over a period of 3 weeks. This decrease in digestibility was of a similar or even greater magnitude than that of those tillers that did grow and increase in size.

In the canopy, therefore, tiller digestibility decreased with age, whether the tiller developed and increased in size, or whether it remained of constant size. That the digestibility of tillers decreased with age was expected; but why certain tillers did not develop and decreased in digestibility required explanation.

The reason for both these phenomena is thought to be related to the effects of shading. Shading leads to lower rates of photosynthesis (Woledge, 1978), and thus to a decrease in growth rates, and when severe can lead to tiller death (Ong, 1978; Langer et al., 1964). Shading also causes decrease of total non-structural carbohydrate content and increase in lignification, thus resulting in lower digestibility (Wilson & Wong, 1982).

Another factor involved is ageing. A small tiller present on Day 42 may appear physiologically "young", but chronologically it is at least 3 weeks old. Digestibility decreases with age, so that part of the tiller's decrease in digestibility can be explained by its age, however the effect

of age is small in comparison to other factors such as temperature or morphological factors such as the level of insert of the leaf (Deinum, 1976).

Leafblade and stem digestibility seem to be affected differentially by the shading. Considering the small tillers only (5-10cm), the digestibility of the leafblades decreased faster with time than that of the stem possibly because of less lignification of the latter. This suggests that shading affects the digestibility of leafblades more than that of the stem.

Since the larger tillers have a greater portion of their leaf surface exposed to higher light intensities, the leaf digestibility of the taller tillers on Day 42 was higher than that of the smaller tillers. The higher leaf digestibility of the taller tillers compensated for the lower stem digestibility, as compared to the small tillers, and may explain why whole-tiller digestibility was not affected by tiller length when compared for each date separately.

The results from the digestibility analyses of plants which grew in pots (Exp. 3) were similar to those of the field. Mutual shading between plants growing in the pots was probably less severe due to the wider spacing between the pots as compared to the field. Additionally, tillers were much shorter in pots than in the field, which may explain the overall higher digestibility values as compared with the field.

However, tiller death was found to occur also in the pots (Fig. 5B), so shading within the plants must have been

of sufficiently large magnitude to retard the growth of small tillers. The digestibility results showed, as in the field, a decrease in tiller digestibility both in tillers increasing in size, as well as in those which were prevented through shading from increasing in size.

6.7 Prediction Of Canopy Digestibility

Our original hypothesis was that tiller digestibility is directly related to its physiological age as expressed through its length (or weight), and that canopy digestibility can be estimated by taking into account the canopy structure, i.e. the distribution of the tiller number according to length (or weight) with known digestibility.

This hypothesis was the assumption made by Kalu & Fick (1981) as the basis of their growth (or development)-stage classification with respect to the digestibility of alfalfa. They classified alfalfa stems according to size and morphological development, and calculated the mean stage of development. The contribution of each class to the mean was weighted by either the number of stems (mean stage by count) or by the dry weight of the stems (mean stage by weight) in that class.

A highly significant relationship was found between the mean stage by weight and canopy digestibility of alfalfa (Kalu & Fick, 1981). However, since they did not analyze the digestibility of each class separately, they did not prove

the existence of a consistent relationship between stage of development and digestibility of alfalfa stems. Also in our experiment with hybrid pennisetum, the calculation of a mean developmental stage by weight (according to tiller length distribution) would have shown that developmental stage is negatively correlated with digestibility. Yet factually no consistent relationship was found between the developmental stage of the tillers and their digestibility. Thus care must be taken when attempting to relate canopy digestibility with the mean stage of development of the component tillers (or stems).

The absence of a clear relationship between tiller length and digestibility of hybrid pennisetum meant that we were not able to incorporate the prediction of canopy digestibility in the SIMPIL model. This presumably would be possible if we could have predicted the digestibility of each tiller in the canopy, taking into account the effect of the differing intensities of light within the canopy. This requires additional research into the inter-relationships between light intensity and tiller digestibility. However, this was beyond the aim of the present study and was not pursued.

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8 Appendices

I Simulation program SIMPIL

```

100 ! "SIMPIL" - PROGRAM FOR SIMULATION OF HYBRID PENNISETUM
110 EXTEND
\
120 INPUT "DATE, TEMP, AND RAD INPUT FILE NAME: "; C$
\      !TEMP=MEAN DAILY VALUE, DEGREE CELSIUS
\      !RAD =TOTAL DAILY RADIATION, CAL/(750*CM**2)
\ INPUT "YIELD OUTPUT FILE NAME: "; Y$
\      !YIELD PER CUT AND CUMULATIVE, G/PLANT
\ INPUT "TILLER-DISTRIBUTION FILE NAME: "; T$
\      !NO. TILLERS & MEAN TILLER WEIGHT PER CLASS, PER PLANT
\ INPUT "PLOTING DATA FILE NAME"; P$
\      !WEIGHT AND NO. TILLERS PER PLANT
\ OPEN C$ FOR INPUT AS FILE#1
\ OPEN Y$ FOR OUTPUT AS FILE#2
\ OPEN T$ FOR OUTPUT AS FILE#3
\ OPEN P$ FOR OUTPUT AS FILE#4
\
140 DIM FSTUB(19),STUB(19),NTIL(20),WTIL(20),AVWT(19),MAXWT(19)
\
150 READ AVWT(I) FOR I=1 TO 18
\ DATA .02,.17,.47,.91,1.5,2.22,3.08,4.07,5.2,6.47,8.62,
\      12.0,15.8,20.2,25.2,33.6,46.5,61.6
160 READ MAXWT(I) FOR I=1 TO 18
\ DATA .08,.31,.68,1.19,1.84,2.63,3.56,4.62,5.82,7.15,
\      10.2,13.8,18.0,22.6,27.8,39.8,53.8,69.9
170 READ FSTUB(I) FOR I=1 TO 18
\ DATA 0,.5,.66,.73,.77,.8,.82,.84,.85,.87,.88,.89,.9,
\      .91,.92,.92,.93,.94
180 READ K, FLEAF, FDEATH, FDIE, FTRANS, FBASAL, FTILIN, AREA
\ DATA 0.5, 1.2, 0.02, 0.1, 0.25, 3.5, 0.02, 4200
\
190 PRINT "EXTINCTION COEFFICIENT           =0.5           (K)"
\ PRINT "PHOTOSYN. TISSUE FACTOR           =1.2           (FLEAF)"
\ PRINT "RGR LEVEL FOR TILLER DEATH         =0.02 G/G/DAY (FDEATH)"
\ PRINT "DYING RATE                         =0.1 10%/DAY (FDIE)"
\ PRINT "TRANSFER RATE                     =0.25 25%     (FTRANS)"
\ PRINT "BASAL TILLERS PER DECAPIT.         =3.5           (FBASAL)"
\ PRINT "TILLER INITIATION WEIGHT           =0.02 G       (FTILIN)"
\ PRINT "AREA PER PLANT                     =4200 CM**2   (AREA)"
\
200 PRINT\PRINT "IF YOU WANT TO CHANGE ANY VALUE, DO SO NOW"
\ STOP
210 PRINT#2\PRINT#2, "K=";K;" FLEAF=";FLEAF;" FDEATH=";FDEATH;
\ " FDIE=";FDIE;" FTRANS=";FTRANS;" FBASAL=";FBASAL;
\ " FTILIN=";FTILIN;" AREA=";AREA
\
\
270 PRINT\PRINT "FOR INITIAL TILLER NUMBER AND WEIGHT DATA"
\ PRINT " DO YOU WANT "
\ PRINT " - TO USE STANDARD DATA (PRINT 1)"
\ PRINT " - TO ENTER SPECIFIC VALUES (PRINT 2)"
\ INPUT A% \ IF A%=2 GO TO 340

```

```

310 READ NTIL(I) FOR I=1 TO 5 !INITIAL CANOPY STRUCTURE
\ DATA 100, 100, 14, 7, 1
330 N%=5 \ GO TO 410
\
340 PRINT\PRINT "FOR EACH CLASS, ENTER NUMBER OF TILLERS "
\ PRINT " TO END, ANSWER WITH .0"
370 PRINT \ FOR I=1 TO 18
380 PRINT "FOR CLASS ";I
\ INPUT NTIL(I)
\ IF NTIL(I)=.0 THEN 400
390 NEXT I
400 N%=I-1 !N%=NUMBER OF INITIAL CLASSES
410 WTIL(I)=NTIL(I)*AVWT(I) FOR I=1 TO N%
\
415 INPUT "TREATMENT, CUTTING CYCLE, DAY OF START";T,M,START
\ INPUT#1, DATE UNTIL DATE>=START-1
420 GOSUB 830 !CLEANING HARVEST: DAY 0
430 PRINT "ENTER HERE THE CUTTING SCHEDULE YOU WANT TO FOLLOW."
\ PRINT " USE THE FOLLOWING FORMAT: 440-480 CUT=X \ GOSUB 490"
\ STOP !FOR ENTERING CUTTING SCHEDULE
490 GO TO 1180
\
\
489 !----- CENTRAL PROGRAM -----
\
490 GOSUB 950 !INITIALIZING OF CANOPY
500 FOR DAY=1 TO CUT
510 GOSUB 580 !DRY WEIGHT PRODUCTION
520 GOSUB 780 !TILLER PRODUCTION
530 GOSUB 1010 !DAILY DATA PRINTOUT
540 NEXT DAY
550 GOSUB 830 !HARVEST, CALCULATION OF YIELD
555 GOSUB 912 !HARVEST, DATA PRINTOUT
560 RETURN
\
\
570 ----- SUBROUTINE FOR LEAF-AREA, RGR CALCULATION -----
\
580 INPUT#1 ,DATE,TEMP,RAD,DD
590 IF NTIL(N%+1)>0 THEN N%=N%+1
600 IF N%>5 THEN TILSTOP=1 !STOP TILLERING WITH ELONGATION
610 SUMLFA=0
620 FOR I=N% TO 1 STEP -1
630 IF NTIL(I)=0 THEN 750
640 LAVWT=LOG(WTIL(I)/NTIL(I))
\ WTLF=NTIL(I)*EXP(-0.22+0.85*LAVWT-0.023*LAVWT**2)
\ !LEAF WEIGHT PER CLASS
\ LFA=WTLF*(433-71*LOG(6*I))
\ !LEAF AREA PER CLASS
\ RDD=RAD*EXP(-K*SUNLFA/AREA)
\ !RADIATION INCIDENT ON CLASS
\ SUNLFA=SUNLFA+LFA
\ RGR=-0.0093+(1.0-EXP(-3.5*RDD))*0.0062*TEMP
\ !RELATIVE GROWTH RATE
\ IF RGR<FDEATH THEN GOSUB 930
\ !TILLER DEATH

```

```

700  WTIL(I)=WTIL(I) + RGR*WTLF*FLEAF
      \                                     ! DRY MATTER ACCUMULATION
      \
      \  AVWT=WTIL(I)/NTIL(I)
      \  IF AVWT>MAXWT(I) THEN 740
      \    ELSE IF AVWT<AVWT(I) OR NTIL(I)<4 THEN 750
710  IF I=18 GO TO 550                                     ! FORCE HARVEST WHEN CLASS 18 MOVES TO 19
720  CHTIL=FTRANS*NTIL(I) \ WCHTIL=CHTIL*MAXWT(I)
      \  NTIL(I+1)=NTIL(I+1) + CHTIL
      \  WTIL(I+1)=WTIL(I+1) + WCHTIL
      \                                     ! PARTIAL TILLER NO. & WT. TRANSFER
      \  NTIL(I)=NTIL(I)-CHTIL
      \  WTIL(I)=WTIL(I)-WCHTIL
730  GO TO 750
740  NTIL(I+1)=NTIL(I+1) + NTIL(I)
      \  WTIL(I+1)=WTIL(I+1)+WTIL(I)
      \                                     ! TOTAL TILLER NO. & WT. TRANSFER
      \  NTIL(I)=0 \ WTIL(I)=0
750  NEXT I
760  RETURN
      \
      \
779  !----- SUBROUTINE FOR TILLER PRODUCTION -----
      \
780  IF TILSTOP=1 THEN 810                                     ! NO TILLERING IN SHADE, ELONGATION
      \
790  PROTIL=NTIL(3)+NTIL(4)                                     ! POTENTIAL PARENT TILLERS
      \  INTIL=PROTIL*(TEMP-11.58)/52.63 + 0.2*BASAL
      \                                     ! NEWLY INITIATED TILLERS
      \  NTIL(1)=NTIL(1) + INTIL
      \  WTIL(1)=WTIL(1) + INTIL*FTILIN
      \                                     ! NEW TILLER NO. & WT. ADDITION
800  BASAL=INT(0.8*BASAL)                                     ! DECREASE POTENTIAL BASAL TILLER NO.
810  RETURN
      \
      \
829  !----- SUBROUTINE FOR HARVEST -----
      \
830  MAT STUB=ZER \ BASAL=0 \ YIELD=0 \ NTIL=0
840  FOR I=1 TO 18 \ IF NTIL(I)=0 THEN 870
850  STUB(I)=NTIL(I)*0.2618*(WTIL(I)/NTIL(I))*0.643
      \                                     ! STUBBLE WEIGHT
860  YIELD=YIELD + WTIL(I) - STUB(I)
870  NEXT I
880  BASAL=BASAL + NTIL(I)*FBASAL FOR I=6 TO 18
      \                                     ! POTENTIAL BASAL-TILLER NO.
890  NTIL=NTIL+NTIL(I) FOR I=3 TO 18
      \                                     ! TILLERS LESS THAN 10CM NOT COUNTED
910  TILSTOP=0 \ RETURN
      \
      \
911  !----- SUBROUTINE FOR HARVEST DATA PRINTOUT -----
      \
912  TOTYLD=TOTYLD+YIELD
      \  PRINT#2,"YIELD AT DAY ";DATE;" = ";YIELD*(1-0.8**DAY);TAB(30);
      \    " SUMMED YIELD= ";TOTYLD;TAB(55);" NO. TILLERS= ";NTIL
      \  RETURN

```

```

\
! ----- SUBROUTINE FOR TILLER DEATH -----
\
930 NTIL(1)=NTIL(1)*(1-FDIE)
\   WTIL(1)=WTIL(1)*(1-FDIE)   !REMOVAL DEAD TILLER NO., WT.
\   TILSTOP=1 \ RETURN
\
! ----- SUBROUTINE FOR INITIAL REGROWTH (10 DAYS) -----
\
950 WTIL(1)=STUB(1)+STUB(2) \ WTIL(2)=STUB(3)+STUB(4)
\   WTIL(3)=STUB(5)           !INTACT TILLER RESIDUAL WT.
\   NTIL(1)=NTIL(1)+NTIL(2) \ NTIL(2)=NTIL(3)+NTIL(4)
\   NTIL(3)=NTIL(5)           !INTACT TILLER NO.
970 NTIL(1)=0 FOR I=4 TO 18
980 WTIL(1)=0 FOR I=4 TO 18
990 N%=3 \ RETURN
\
! ----- SUBROUTINE FOR DATA PRINTOUT -----
\
1010 IF DAY<>(INT(DAY/2)*2+1) THEN 1080
\                                     !PRINTOUT ON UN-EVEN DAYS ONLY
1020 NTIL=0 \ WTIL=0
1030 WTIL=WTIL+WTIL(1)*FSTUB(1) FOR I=1 TO 18
1040 NTIL=NTIL+NTIL(1) FOR I=3 TO 18
1060 PRINT#4,T,DATE,TAB(10);NTIL;TAB(20);WTIL*(1-0.8**DAY)
1080 UNLESS DAY=CUT GO TO 1170
1100 FOR I=18 TO 3 STEP -1
1110 IF NTIL(I)=0 GO TO 1150
1120 AVWT=WTIL(I)/NTIL(I)
1140 PRINT#3 T;TAB(3);M;TAB(6);I;TAB(10);AVWT;
\   TAB(16);NTIL(I)
1150 NEXT I
1170 RETURN
\
! ----- OPTION TO CONTINUE -----
\
1180 INPUT"DO YOU WANT TO CONTINUE (Y/N)";I$
\   IF I$="N" GO TO 1190
1185 RESTORE \ CLOSE#1 \ OPEN C$ FOR INPUT AS FILE#1
\   TOTYLD=0 \ GO TO 150
1190 CLOSE 1,2,3,4
1200 END

```

II List of program parameters

AREA: The area available to each plant (cm^2)

AVWT: Average tiller weight, per class (g)

AVWT(I): Defined average tiller weight per class (g)

BASAL: Number of basal tillers that can potentially develop from the total number of decapitated tillers

CHTIL: Number of tillers transferred from one class to the next higher one

CUT: Length of cutting interval, days

DATE: Number of days since start of season

DAY: Number of days from previous defoliation

FDEATH: The RGR value below which tillers die ($\text{g}^{-1}\text{day}^{-1}$)

FDIE: The fraction of tillers that dies per day when the RGR value is below FDEATH

FLEAF: A correction factor for leaf weight, in order to include the weight of the leafsheaths

FSTUB(I): The fraction of the tiller weight left in the field as residual tiller weight. Used as an approximate value for the interim calculations between harvests.

FTILIN: The initial weight for a new tiller (g)

FTRANS: The fraction of tillers transferred from class to class when $\text{AVWT} > \text{AVWT}(I)$

I: Number of class

INTIL: Number of new tillers initiated

K: Light extinction coefficient

LFA: Leaf area per class (cm^2)

M: Cutting cycle number

MAXWT(I): Maximum defined average tiller weight per class
(g/tiller)

N%: Number of tiller classes

NTIL: Summed number of tillers of all tiller classes

NTIL(I): Number of tillers, per class

PROTIL: Number of tillers capable of producing axillary
tillers

RAD: Total daily radiation ($\text{cal cm}^{-2}\text{day}^{-1}$)

RDD: Total daily radiation received per tiller class ($\text{cal cm}^{-2}\text{day}^{-1}$)

RGR: Relative growth rate ($\text{g g}^{-1}\text{day}^{-1}$)

STUB(I): Stubble weight per class (g)

SUMLFA: Cumulative leaf area from tallest tiller class down
(cm^2)

T: Cutting treatment

TEMP: Average daily temperature ($^{\circ}\text{C}$)

TILSTOP: A parameter which signifies a stop in tiller
initiation

TOTYLD: Seasonal yield (g/plant)

WCHTIL: The weight of tillers transferred from one class to
the next higher one (g)

WTIL: Summed weight of all tiller classes (g)

WTIL(I): Weight of tillers per class (g)

WTLF: Weight of leaves per class (g)

YIELD: Summed weight of all tiller classes on day of harvest
less stubble weight (g)

PART 6. FORAGE QUALITY ASPECTS

OXALATES IN HYBRID PENNISETUM

ABSTRACT

The Oxalate content of young plants was higher than that of old ones, and of leaves higher than that of stems. No differences in oxalate content were found between the hybrid 23AxN23 and its male parent N23. The highest total oxalate content of field grown hybrid Pennisetum plants was 2.5% (d.w) and that of soluble oxalate did not exceed 1%. ^{These values} are not sufficiently high to be considered hazardous even with high application of nitrogen fertilizer. The highest total oxalate content in field grown hybrid Pennisetum plants was 2.5% (d.w) and that of soluble oxalate did not exceed 1%.

INTRODUCTION

Certain forage species contain relatively high oxalate levels (>5% of the dry weight). Such high concentrations were reported to be responsible for fatalities of cattle grazing the tropical grass Setaria sphacelata cv. Kazungula (Jones et al 1970). Acute signs of hypocalcaemia and deposition of calcium oxalate crystals in the kidneys have been reported by Seawright et al (1970).

Because plants maintain a balance between positively and negatively charged ionic constituents (Wit C.T. de, et al 1963), massive uptake of

anions, mainly as NO_3^- by the roots followed by their reduction to organic N forms in the leaves, results in a surplus of inorganic cations over inorganic anions. Organic acids accumulate as a consequence of the excess cations in the leaves. Some of these organic acids may be immobilized by precipitation of insoluble salts in the vacuole (Osmond 1967). Ca-oxalate is probably the most common insoluble salt. Oxalate can also be found in the form of sodium or potassium salts. Schneider et al (1970) found a significant correlation between potassium and oxalate content of pearl millet.

Jones and Ford, (1972a) measured the water-soluble oxalate content of various tropical grasses. Four setaria varieties showed the highest soluble oxalate level of all grasses tested.

The oxalate ranking was 3.1-4.2 and 2.8-3.8 % in the leaf blades of setaria in the summer and autumn respectively. Pennisetum clandestinum (Kikuyu) had only 0.72%. In contrast, Pennisetum purpureum (napiergrass) harvested between 6 to 10 weeks of age, had an oxalic acid content not less than 2.5% (Garcia-Rivera and Morris, 1955). It is of interest to note that grass genera which have a cell sap pH of less than 6 have also a high oxalate content. Setaria, Pennisetum and Cenchrus belong to this group (Dougall and Birch, 1966).

We considered it important to make a survey of the oxalate content of hybrid Pennisetum accessions as part of the evaluation program.

MATERIALS AND METHODS

Total and soluble oxalates were analysed following the method of Moir (1953) on samples of leaves, stem + leaf sheaths and whole plants from the following experiments:

- (a) Temperature response study.
- (b) Development and accumulation of dry weight following undisturbed growth in the field.
- (c) Effect of amount and frequency of irrigation.
- (d) Seven week old interspecific hybrid 23A x N23 and its male parent N23.

RESULTS AND DISCUSSION

The highest total oxalate content in field grown plants was 2.5% (d.w. basis) and that of soluble oxalate did not exceed 1%. In contrast, the plants grown in the phytotron accumulated much higher concentrations of oxalate.

Differences in oxalate levels between the hybrids grown in the field were small, and were lower than those reported by Garcia-Rivera and Morris, (1955). Differences in oxalate levels between different cultivars may be due to genetic variability as is known for Setaria sphacelate cultivars collected from different sources (Hacker, 1974).

The effect of age and canopy structure

The total and soluble oxalate content of leaf blades and of stems of hybrids 17 and 20 during undisturbed growth are shown in Figs. 1a and 1b. Oxalate content was higher in leaves than in stems, and this confirms the results of Middleton and Barry (1968) for other tropical grasses grown in

Fig. 1. Distribution of total (A) and soluble oxalates (B) between leaves and stems of two pennisetum hybrids.

Leaf 23AXN17 ———— ☆
 " 23AXN20 ———— +
 Stem 23AXN17 - - - - - ◇
 " 23AXN20 - - - - - △

Fig. 2. Distribution of total (A) and soluble oxalates (B) between leaves and stems of hybrid 23AXN3 and its male parent N23 as related to leaf and internode position along the stems.

Leaf N23 ———— □
 " 23AXN23 ———— ×
 Stem N23 - - - - - ◇
 " 23AXN23 - - - - - ×

Queensland, Australia. The rate of decrease in both total and soluble oxalates with time, was similar in leaves and in stems, indicating low oxalate translocation, possibly due to the rapid precipitation of oxalate salts in the vacuoles of the leaf blade cells.

Oxalate concentrations in the upper-most leaf blades and their sheaths, and in lower leaf blades and stem internodes marked -1 to -4 according to their position from the upper-most leaf downwards were determined. The analyses were conducted on 7 week old plants of hybrid 23A x N23 and its male parent, napiergrass N23. The results are shown in Figs. 2a and 2b. No differences were found in total and soluble oxalate content between the leaves of napiergrass and the hybrid. Napiergrass stems had a higher oxalate content than stems of the hybrid. Mean total oxalate content in the leaves of both, ranged between 1.8% (d.w.) in the upper-most leaf to 2.3% in leaf -4. This is in agreement with the results of Roughan and Warrington (1976) for setaria. In contrast, the upper-most leaf had a relatively high oxalic acid content, but similar concentrations were found in leaves in positions -1 to -4 below the upper-most leaf. The younger stem nodes, however, had significantly higher concentration of both total and soluble oxalates than the older nodes.

It appears that oxalate concentration decreases with plant age and with increasing number of stems per plant (Fig. 3). However, the low oxalate concentration in the hybrid, in general, and of the leaves in particular, justifies the continuation of the breeding program towards a more leafy type of hybrid Pennisetum plant.

Fig. 3. Relationship between total and soluble oxalates and stem/leaf weight ratio. thermal adaptation study B.
 ○ + 32/22°C
 □ Δ 27/17°C

Fig. 4. Soluble oxalate content in plants of hybrid pennisetum differing in nitrogen content.
 + thermal adaptation study B. (32/22 and 27/17°C)
 □ undisturbed growth
 Δ response to irrigation

Relationship between oxalate content and nitrogen fertilization.

Among the principal growing factors, nitrogen nutrition may have the most significant influence on the oxalate content. A great part of the synthesis of organic anions compensates for the reduction of nitrate by nitrate reductase. Forage grasses in Israel are fertilized with high amounts of nitrogen, and a seasonal application of 600 kg N ha⁻¹ is not rare. It was therefore of interest to investigate whether the oxalate content in hybrid pennisetum is affected by nitrogen fertilization.

Since N fertilization trials were not carried out in the program, the plant material for oxalate determinations was taken from experiments where plants had different N content. Oxalic acid increased with the increase of N content. N content higher than 2.5% was not followed by more oxalic acid synthesis (Fig. 4). Jones and Ford (1972b) found that the oxalate content in N- fertilized Setaria sphacelate was 70% higher than non N-fertilized plots. Roughan and Warrington (1976), also working with Setaria, found similar oxalate concentrations whether ammonium, urea or nitrate where the source of N. According to our results the asymptotic curve which was obtained in relation to N content and the low content of soluble oxalate in field grown hybrids assured that no hazardous amounts of oxalates accumulate even under intensive nitrogen fertilization.

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PART 7. BREEDING ASPECTS

A . PERFORMANCE OF HYBRID PENNISETUM 23A x N23 COMPARED WITH ITS MALE PARENT NAPIER GRASS (N23)

INTRODUCTION

In view of recent efforts made in the production of hybrid Pennisetum cultivars, with the aim of obtaining a grass combining the nutritive quality of pearl millet with the regrowth capability and yields of napier grass, it was considered of interest to compare the hybrid with its male parent.

The two genetically related grasses were compared in the following aspects:

1. Total dry yield, digestible yield, percent digestibility, and percent dry matter.
2. Accumulation of dry matter in the single-plant and tiller number.
3. Relationship between tiller weight and tiller length, and between leafblade weight to tiller weight.
4. Proportion of decapitated and dead tillers and the distribution of tiller and plant weight according to tiller size.
5. Location of the apical meristem (i.e. distance between the apex and the ligule of the uppermost leaf).

MATERIALS AND METHODS

Plants of hybrid Pennisetum (23AxN23) and napiergrass (N23) grown in the field were subjected to cutting intervals of 3 or 6 weeks during a period of 130 days. The plants were spaced 60x60cm. The experiment was of a split-plot design with 2 blocks (replicates), each subdivided into six main plots (grass species), three for each of the grasses, the location of each having been determined at random. Each main plot was divided into two sub-plots for the two cutting frequencies. Each sub-plot measured 6x12m. The fields were sprinkler-irrigated and fertilized at rates ensuring maximum growth.

Every 10 days one plant, chosen randomly, was harvested from each sub-plot. It was weighed green, and the total number of tillers counted. Approximately one-third was taken for determining the percentage of dry matter. The remaining two-thirds were used to determine tiller length distribution as follows:

1. The length of each tiller was measured from the cutting level to the top ligule (i.e. the youngest fully-expanded leaf).
2. They were then graded according to their length into 4 size classes, each 10 cm starting from 0 forming a separate class (i.e. class 1 from 0 to 10 cm long, class 2 from 10 to 20 cm, class 3 from 20 to 40 cm and class 4 from 40 cm onwards).
3. For each size class the following was recorded: (a) Number of intact tillers, (b) Number of decapitated tillers, and (c) Number of dead tillers, i.e. those of which the youngest leaf is dead, which indicates the lack of apical activity, (d) Dry weight of leafblades per tiller, and (e) Dry weight of stem+sheath per tiller. In addition, the position of the apical meristem in the elongating tillers was determined by

cutting tillers taller than 25 cm longitudinally and measuring the distance between the apical meristem and the uppermost visible ligule.

At the end of each cutting cycle the plants were cut by a forage-mower, and the total fresh yield per sub-plot was weighed. A representative sample of approximately 600g was taken from the cut herbage of each subplot, it was dried to constant weight and the percentage of dry matter was determined. Samples of the three sub-plots per block were mixed in equal quantities, ground, and submitted to digestibility analysis. Drying of the plant material was at 70°C in a forced-air oven. The in vitro dry matter digestibility (IVDMD) was carried out according to the Tilley & Terry two stage technique.

Data transformations were made before statistical analysis: The mower yields obtained at the end of the cutting interval were divided by the number of growing days to obtain the daily crop growth rate (CGR), enabling comparison of the two cutting treatments. The digestible yield was calculated by calculating the average yield per block and multiplying it by the digestibility per block. This value was then similarly divided by the number of growing days to obtain the average digestible matter growth rate (DCGR).

The weight per plant and number of tillers per plant were converted to natural log values. This was found to be necessary following analysis of the relationship between the value of the mean and its standard deviation. For percentages the angular transformation was applied.

RESULTS

Total dry matter and digestible yields

Both hybrid Pennisetum and napiergrass had a higher average growth

rate in the 6 wk than in the 3 wk cutting intervals, but between the grasses there was no significant difference (Table 1). The digestibility of the 3-wk treatment, however, was significantly higher, so that the rate of digestible dry matter accumulation was similar for all treatments.

Table 1. Crop Growth Rate (CGR), Digestible Matter Growth Rate (DCGR), Percentage Dry Matter (PDM) and in vitro Dry Matter Digestibility (IVDMD) of hybrid pennisetum and napiergrass under 3 and 6 weeks cutting interval.

	CGR (gm ⁻² day ⁻¹)	DCGR (gm ⁻² day ⁻¹)	PDM (%)	IVDMD (%)
		<u>3 weeks</u>		
Hybrid	17.9bc	11.5a	13.1a	64.3a
Napier	16.1c	10.7a	12.9a	65.0a
		<u>6 weeks</u>		
Hybrid	20.5a	12.1a	13.5a	59.5b
Napier	18.9ab	11.4a	13.6a	60.2b

Numbers followed by the same letter are not significantly different (p=0.05). Means of six 3-weeks and five 6-weeks intervals (six replications per interval).

Dry matter accumulation in the single plant and number of tillers

Hybrid Pennisetum and napiergrass were very similar in the accumulation of dry matter as well as in the number of tillers per plant in the 3-wk interval treatment (Figs. 1, 2). In the 6 wk treatment, however, the number of tillers per plant was significantly higher for hybrid Pennisetum, though the dry weight per plant was similar. From the first cutting to the third, the number of tillers per plant decreased in the hybrid while it increased in the napiergrass plants (Figs. 3, 4). This interaction was highly significant.

Fig. 1. Accumulation of dry matter in plants subjected to 3-week cutting intervals.

Fig. 2. Increase in number of tillers in plants subjected to 3-week cutting intervals.

Fig. 3. Accumulation of dry matter in plants subjected to 6-week cutting intervals.

Fig. 4. Increase in number of tillers in plants subjected to 6-week cutting intervals.

Relationship between tiller weight and tiller length, and between leaf blade weight and tiller weight.

The relationship between the length of a tiller and its weight (wt_{tl}) was characterized by the following equation:

$$\ln(wt_{tl}) = -3.291 + 1.318 \times \ln(\text{length}) \quad (r^2 = 0.93, \text{d.f.} = 42)$$

The slope was identical regardless of the plant species, cutting interval, or their interaction.

Between the leaf blade weight (w_{leaf}) and tiller weight (wt_{tl}) the following relationship was found:

$$\ln(w_{\text{leaf}}) = -0.236 + 0.861 \times \ln(wt_{tl}) - \ln(wt_{tl})^2 \quad (r^2 = 0.99, \text{d.f.} = 42).$$

Again there was no difference between the plant species, nor between the cutting intervals.

Proportion of decapitated and dead tillers and the distribution of tillers and plant weight according to tiller size groups.

In both cutting intervals the tiller number distribution of the two grasses was no similar (Table 2). Napiergrass tended to have relatively more tillers in the higher tiller-size groups.

The distribution of plant weight among the tiller groups (Table 3) was related to tiller number distribution. This was more pronounced in the taller groups due to the higher average tiller weight of the taller tillers.

Table 2. Distribution of tiller number per plant (%) according to their length on the day of cutting (means of five, 3-weeks and three, 6-weeks intervals).

	Tiller length group (cm)			
	<10	10-20	20-40	>40
3 weeks				
Hybrid	63.3	28.7	7.91	-
Napier	46.7	34.9	16.7	1.69
6 weeks				
Hybrid	32.4	21.7	21.0	24.9
Napier	27.4	16.2	13.4	43.0

Table 3. Distribution of plant weight (%) according to tiller length groups on day of cutting (means of five, 3-weeks and three, 6-weeks intervals).

	Tiller length group (cm)			
	<10	10-20	20-40	>40
3-weeks				
Hybrid	35.1	43.9	21.0	-
Napier	17.8	36.1	41.6	4.5
6-weeks				
Hybrid	5.5	9.1	23.5	61.9
Napier	3.2	3.6	7.2	86.0

The proportion of decapitated tillers per size group was similar for the two grasses in each of the cutting intervals (Table 4). It was higher in the 3-wk than in the 6-wk interval treatment, though its significance was not tested. The proportion of dead tillers was the same for both grasses in the 3-wk intervals, but it ^{was} higher in napiergrass than in the hybrid in the 6-wk intervals, where it occurred even in the tallest two groups (Table 5). This difference was highly significant.

Table 4. Percentage of decapitated tillers of different size groups at the end of the cutting interval of hybrid pennisetum and napiergrass (means of five, 3-weeks and three, 6-weeks intervals).

	Tiller length group (cm)			
	<10	10-20	20-40	>40
3-weeks				
Hybrid	0	15	91	0
Napier	0	10	88	100
6-weeks				
Hybrid	0	0	78	100
Napier	0	0	73	100

Table 5. Percentage of dead tillers of different size groups at the end of the cutting interval of hybrid pennisetum and napiergrass. (means of five, 3-weeks and three, 6-weeks intervals)

	Tiller length group (cm)			
	<10	10-20	20-40	>40
3-weeks				
Hybrid	3	0	0	0
Napier	3	0	0	0
6-weeks				
Hybrid	70	48	1	0
Napier	80	54	48	1

Position of the apical meristem within the tiller.

Data from the end of the second and third 6-wk cutting intervals were collected, so that the two could be compared with each other at the same date. Since there was no significant difference between the two dates, the average values are presented in Table 6.

The apical distance was significantly shorter in the 3-wk interval than in the 6-wk interval. However, there was no difference between the two grasses.

Table 6. Position of apical meristem within elongating tillers of hybrid pennisetum and napiergrass (mean of 10 tillers)

Grass	Cutting interval		Mean
	3-weeks	6-weeks	
Hybrid	17.9*	24.2	21.1
Napier	20.0	23.2	21.6
Mean	19.0	23.7	21.3

* Distance of apical meristem below uppermost ligule (cm).

DISCUSSION

Total dry matter production and digestibility were not different between napier grass and hybrid Pennisetum when cut at the same frequency. Both yielded significantly more total dry matter under the 6-wk than under

the 3-wk cutting frequency, though total digestible dry matter yields were not different due to the concomitant decrease in digestibility.

Analysis of single-plant weight and tiller number from plants sampled at 10 day intervals showed similar dry matter accumulation for both grasses. In both there was an initial lag of regrowth following a 6-wk cutting interval, while following a 3-wk interval there was almost no lag. Both also showed a decrease of tiller number per plant towards the end of the 6-wk intervals. Napier grass differed from hybrid Pennisetum in that the number of tillers per plant increased from the first to the third interval, while that of hybrid Pennisetum remained constant or even decreased. This may be related to the more pronounced tendency for napier grass plants to expand at the plant base. It should be noted that the lower tiller number in the first interval was associated with the highest weight per plant.

Morphologically hybrid Pennisetum and napiergrass are similar. Even though the two plants can be distinguished visually with ease, the tillers of the plant were undistinguishable in terms of the relationship between the weight of the tiller and its length, or between leaf weight and tiller weight. The latter relationship is probably not specific to these two genetically related grasses, since in a trial with several different napier grasses the same relationship was found. The tiller weight/length relationship did, however, differ greatly between the napiergrasses.

An additional point of interest, related to regrowth capability, is the length of the apical distance. This was similar for the two grasses, although was significantly influenced by cutting interval.

The hybrid seems to differ from its male parent in that it tends to produce a larger number of tillers, whereas the growth rate per tiller is

less, thus creating plants with a higher proportion of tillers in the lower size groups. In the field the hybrid was always of a shorter stature than napiergrass.

Associated with this tendency of napiergrass to produce larger and taller tillers is the higher proportion of dead tillers among the small tillers. This is probably due to the intensive shading and competition for light, which hardly occurs in the 3-wk old canopy.

There is no difference in the proportion of tillers decapitated in each of the size groups. This is related to the fact that the location of the apical bud within the tiller was similar in both grasses (Table 6).

There was a difference in digestibility of about 5% units between the two cutting intervals, a difference which is not very big, considering the large differences of canopy structure between the 3-wk and the 6-wk intervals. This lack of sensitivity in canopy digestibility to canopy structure may explain why no differences in digestibility were found between the two grasses in spite of the higher proportion of tall, stemmy tillers in the napier grass.

CONCLUSIONS

Although the two grasses differed in their form of growth (napier grass having a higher proportion of tall tillers, this did not express itself in the total yield or in digestibility of the canopy. The tendency to produce taller tillers is not related to a difference in the weight/length relationship of the tillers, and is thus probably due to other differences between the two grasses.

The hybrid seems to be more similar to its male parent than to pearl millet since it did not differ from the former in growth rate, digestibility, tillering capacity, or regrowth rate.

B. Development of New Interspecific Hybrid Combinations for High Yields of Quality Forage

The pearl millet (Pennisetum americanum L. Leeke (2n = 14) x napiergrass (P. purpureum Schumach, 2n = 28) interspecific cross was first reported in 1944 (1) and has been since studied by a number of research groups (2, 3). The interspecific hybrids produce high yields of dry matter that are of high quality if properly managed. The interspecific hybrids also have the advantage of producing high quality forage in the U.S. during late August until the end of November during a period when most tropical forages have greatly decreased in quality and yield (2). The interspecific hybrids made with the standard cytoplasmic male sterile 'Tift 23' will begin flowering in late September. It would be desirable to prevent flowering to keep the plants vegetative which would favor the maintenance of high forage quality.

The objectives of this aspect of the research program were (A) to develop late-maturing, short-day sensitive (SDS) cytoplasmic male sterile (cms) lines and (B) to evaluate pearl millet x napiergrass interspecific hybrids. The short-day sensitive cms lines are proposed for use as female parents of hybrids to produce later maturing hybrids resulting in higher quality and yield of forage.

Short Day sensitive Lines - Genes for short day sensitivity were used from two different African varieties: 'Maiwa' and 'Sefa'.

Tift inbred 'Tift 23' will flower in 75-80 days after planting when planted at the first of June. 'Maiwa' will begin to boot at Tifton, Georgia at the end of November (at frost time) regardless of when it is planted during spring or summer. Therefore, crossing has to be done in the greenhouse during the winter. A number of single plant selections were made within 'Maiwa' and used to pollinate cms 'Tift 23DA₁'. This process was continued for two generations in the greenhouse to find genotypes that would maintain the male sterility

of Tift 23DA₁. Completely male-sterile SDS lines that were developed were then used as female parents and pollinated with standard pearl millet inbreds and napiergrass pollen. In 1983, a non-replicated spaced plant (1 m in the row and 2 m between rows) yield trial (because of limited seed supplies) was conducted to begin measuring effects of the SDS lines as female parents in crosses with napiergrass (Table 1). A single harvest was made in October of plants in the heading stage, that had been established in June. Crosses involving N8 and N39-2 as pollinators on SDS lines produced higher mean dry matter yields and higher mean in vitro dry matter digestibility values than crosses with Tift 23A as female parent. There appeared to be small or no differences when N69 was used as a pollinator indicating genotype interaction(s). Certain pearl millet x napiergrass combinations are better than others. The very low (0.5 kg/plant) yields for some plants are common in these interspecific crosses because of the heterozygosity of napiergrass. The low yielding plants would not be observed in a seeded yield trial because the vigorous plants would crowd them out. Although there is a range in dry matter percent for hybrids in Table 1, most of this is probably due to maturity. This is also reflected in the hybrids made with DLS females (more vegetative) being lower in average dry matter percent. In 1974 (Table 2), hybrids in entries 55, 60, 74, to 77 and 81 were made using the standard cms female, Tift 23, while entries 63 to 67 and 78 to 79 were made using newly developed short-day sensitive cms lines. SDS lines pollinated with pearl millet inbreds 383 and PS209 produced significantly ($P = 0.05$) more dry matter than when the standard 'Tift 23' was pollinated with the same inbreds. These data indicate a positive yield advantage to using the SDS lines as females in pearl millet hybrids.

In the pearl millet x napiergrass crosses (Table 2), hybrids using the standard cms line (entries 74 and 76) crossed with N14 yielded significantly

more dry matter than when the SDS line was used as female (entry 78). There were no differences in dry matter yields of hybrids when N20 was used to pollinate either the standard or SDS females. There appears to be genotype interactions in these crosses.

The greatest advantage of delaying flowering of hybrids by using DLS female parents would be to maintain higher forage quality and extending the period of forage production. Delaying flowering would also favor easier forage management to maximize production of quality forage.

Genes controlling SDS from the 'Se fa' variety were transferred to Tift 23 through five backcrosses. The resultant lines which are similar to Tift 23 but reach anthesis 45-60 days later than standard Tift 23 have been used to pollinate cms Tift 23DA to produce a later maturing cms line. In another year, late cms lines should be ready for testing in hybrid combination.

An important consideration in the development of SDS lines is whether they can be used in the regular seed producing areas to produce commercial hybrids. The 'Maiwa' lines could not be used in the regular seed producing areas because when days became short enough to induce flowering, frosts would kill the plants. Seed production on the 'Maiwa' lines would need to be done in a tropical area where days of 11 hours or less are frost-free. The 'Se fa' derived lines with 'intermediate' SDS could be used in the regular seed producing areas. Lines developed from both SDS sources are highly rust resistant. Preliminary data indicate that the newly developed SDS lines can be used to advantage in both pearl millet hybrids and pearl millet x napiergrass interspecific hybrids to improve dry matter yields and/or quality. The lines need to be tested at least another couple of years before they are considered for release.

Pearl Millet x Napiergrass Hybrids - The data in Tables 1, 2, and 3 indicate that the pearl millet x napiergrass interspecific hybrids produce significantly more dry matter yield than the best commercial pearl millet hybrid (Gahi 3). The data also shows that these interspecific hybrids produce most of their quality forage from mid-summer through the fall when there is a need for high quality forage. Although all of the napiergrass pollinators appeared to produce excellent hybrids, N14 consistently produced the highest yielding hybrids. The pearl millet x napiergrass interspecific hybrids hold great potential for continued increase in production of quality forage.

Table 1. Dry yield, % dry matter and % IVDMD of pearl millet x napiergrass crosses using standard 23A or short day sensitive (DLS) females in crosses.

1983 number	Pedigree	Number plants	Dry matter yield, kg/plant			% dry matter			% IVDMD					
			$\bar{x}$	Range	SE	CV	$\bar{x}$	Range	SE	CV	$\bar{x}$	Range	SE	CV
658	DLS A x N8	113	7.7	0.5 - 28.9	0.6	84	19	13 - 27	0.3	13	58.8	46.1 - 67.4	0.64	8
663	23A x N8	129	4.7	0.5 - 22.0	0.4	87	21	15 - 33	0.6	18	55.9	43.4 - 80.1	0.91	11
659	DLS A x N39-2	131	6.7	0.5 - 18.6	0.3	57	22	16 - 27	0.3	11	55.5	45.3 - 64.7	0.70	9
664	23A x N39-2	8	3.7	0.5 - 8.6	1.1	81	26	19 - 37	2.1	23	46.4	38.3 - 57.1	2.33	14
661	DLS A x N69	128	5.4	0.5 - 16.4	0.4	72	21	16 - 26	0.3	12	55.4	43.6 - 66.1	0.74	10
666	23A x N69	137	5.7	0.5 - 15.7	0.3	62	22	14 - 27	0.6	22	57.6	42.5 - 64.5	0.62	8

Table 2. 1984 dry matter yields of hybrids using normal Tift 23A and short day sensitive lines as females.

1974 Entry	Cross	Dry matter yield (kg/ha) on: ‡				Total
		6/27	7/26	9/06	11/13	
55 ⁺	23A ₁ x I383	4313	5906	4167	963	15,312
60 ⁺	23A ₁ x PS209	6327	6309	6015	2195	17,455
63 ⁺	83-23 x I186	4466	5284	4032	1893	15,778
64 ⁺	83-24 x I383	2853	5987	4677	3761	17,211
65 ⁺	83-24 x PS209	1627	6921	5743	6810	21,086
67 ⁺	83-24 x I186	4314	5708	5051	2292	17,573
74	23A ₁ x N14	1687	6977	7010	7032	22,664
75	23A ₁ x N20	2003	6449	7288	5466	21,071
76	23A _m x N14	1525	6115	8117	7270	23,018
77	23A _m x N20	1966	5173	6259	5573	18,896
78	83-25 x N14	490	4759	7032	6585	18,831
79	83-25 x N20	1318	5084	6221	6712	19,300
81 ⁺	23DA ₁ x I186 (Gahi 3)	4346	6083	4118	1257	15,687
	5% LSD	794	657	878	1209	1,808
	SE	634	525	701	958	1,437
	CV	16	9	16	52	9

⁺ Pearl millet hybrids, all others pearl millet x napiergrass hybrids.

‡ Test part of a 9 x 9 lattice square design with 5 replications.

Table 3. 1982 dry matter yields of pearl millet x napiergrass interspecific hybrids

1982 Entry	Cross	Dry matter yield (kg/ha) on: ‡			
		7/08	8/16	10/08	Total
52	23DA x N8	3912	10,240	4893	19,044
53	23DA x N14	2465	9,579	7030	19,074
54	23A x N8	2565	10,676	7415	20,656
55	23A x N14	2748	11,807	8500	23,055
56	23A x N43	4049	7,934	5872	17,855
80 ⁺	Gahi 3	9390	7,302	1404	16,691
5% LSD		1001	1,110	859	1,784
SE		799	887	685	1,426
CV		10	13	41	9

⁺ Commercial pearl millet hybrid

[‡] Test part of a 9 x 9 lattice square design with 5 replications

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PART 8. PRODUCTION OF HYBRID SEED

FLOWERING OF NAPIERGRASS AND OF PEARL MILLET, AND SEED PRODUCTION OF THEIR HYBRIDS.

The effect of daylength on the flowering of napiergrass.

Plants of a number of napiergrass lines in pots were exposed to different daylength regimes. In the first years trial (Fig.1a) N-20 and N-74 responded similarly in that from 8 to 11 hours of daylight, the number of days erequired for flowering increased from 27 to 33 days. Line N-17 on the other hand required 34 to 40 days to reach flowering at the identical daylength regimes of 8 to 11 hours.

In the second year trial (Fig.1b) the daylength regime was extended to 13 hours and additional lines were tested which also enabled to determine the critical daylength for flowering . Under the regime of 12 hours daylength, 39 to 48 days were required for flowering depending on the line; N-74 was the earliest , and N-17 was the last to flower. No flowering occured in any of the lines at the daylight regimes of 13 hours.

It was concluded that the critical daylength for flowering of the napiergrass lines investigated is between 12 and 13 hours. This

was further ascertained under field conditions at the Yotvata site ($30^{\circ} 20'$) for which the daily course of temperature and daylength are represented in Fig. 2. The arbitrarily chosen daylength for flower induction of 12.5 hours occurs at that location from Sept. 9 onwards. Cuttings from the same lines from which flowering data are presented in Fig. 1b were planted at the end of July 1982 and their flowering response was recorded during a 3-year period. During 1983 and 1984, the plants were cut during July of each year, early enough in the season to avoid the possible effect of defoliation on flower initiation. Lines N-74, N-51 and N-20 flowered at an average of 46, 49 and 53 days, respectively, counted from Sep. 9 onwards, the date from which daylength becomes shorter than the 12.5 h and was assumed to induce flowering. It took line N-23 an average of 81 days to flower. Generally, yearly variation in the time of flowering of identical lines was very small particularly in the early-flowering lines N-74 and N-51. Line N-17 failed to flower during the second and third year for as yet unclear reasons.

Fig. 1. The effect of day length on the flowering of different Napier lines growing in the open and covered with black cloth according to day length regimes.

A. 1981, B. 1982.

Fig. 2. The course of mean daily maximum ($\circ$) and minimum ($+$) temperatures and day length at Yotvata (30°20').

The effect of temperature and the initial number of leaves on the development and flowering of napiergrass.

Plants of a napiergrass (an Australian cultivar), were grown in pots in the phytotron under flower inducing conditions of 8h daylight at temperatures of 27/22°C (day/night) or 32/27°C and with either 4-5 or 9-10 initial leaves following defoliation.

Temperature did not affect the time required from flower initiation to the start of flowering. However, plants with the greater number of initial leaves reached flowering approximately a fortnight earlier than those with the small number of initial leaves. On the other hand both factors, temperature and initial number of leaves did affect plant development in terms of the number of leaves and the number of aerial tillers produced during the period of reproductive growth. Plants with the greater number initial leaves growing under the higher temperature regime reached flowering with a greater number of new leaves on the main stem compared with those growing under the lower temperature regime and the small number of initial leaves. The average rate of appearance of new leaves until flowering was 3 and 3.5 days under the high and the low temperature regimes, respectively. Plants with the initial small number of leaves produced on the average

one new leaf each 3.9 days, whereas it took 2.6 days for a new leaf to appear on plants with an initial greater number of leaves.

The number of days required for flowering of the aerial tillers after the flowering of the main stem was considerably less in plants with the greater number of initial leaves compares with those with the smaller number of initial leaves. This acceleration of flowering due to the greater number initial leaves was not affected by the different temperature regimes. Also the number of flowering aerial tillers, recorded 30 days after the start of flowering of the main stem, was almost double in plants with the greater number of initial leaves, irrespective of the temperature regime.

The effect of different day and night temperatures on several flowering attributes including pollen viability of napiergrass.

Plants of line N-74 were grown in the phytotron under 8 h daylight and exposed to a wide range of day/night temperature regimes viz.: 32/27, 27/27, 27/22, 27/17, 27/12, 22/22, 22/17 or 22/12°C.

In the combinations of the high day and night temperatures, and also of the low day and night temperatures, the plants failed to flower (Fig. 3). At the combination of 27/12°C the plants flowered , however they had no anthers. In all the other cases the plants reached normal flowering and distinctly earlier when the day temperatures were

Fig. 3. The effect of different day and night temperature combinations on the flowering behavior of napiergrass N-74 growing under 8h of daylight

+ flower - no flower x no anthers
() days from induction to flowering

22°C as compared with 27°C irrespective of the night temperatures. Non-flowering plants, due to the high day and night temperatures, had a significantly greater number of leaves per stem, a smaller number of tillers per plant and were taller compared with the flowering plants of identical age. Non-flowering plants, because of the low day and night temperatures, had a significantly smaller number of leaves per plant and were smaller in size. However, they had a greater number of tillers per plant compared with the flowering plants.

The day temperature of 27°C, combined with night temperature of either 22°C or 17°C, significantly shortened the period from the appearance of the flag leaf until the start of pollen shedding, compared with the same above mentioned night temperatures (Table 1). Pollen shedding lasted for 2 days at 27/22°C; whereas under the other temperature combinations it lasted at least 3 days. Pollen viability decreased significantly when the night temperature was lowered from 22°C to 17°C and in more than 30% units at the last day of pollen shedding.

Table 1. The effect of temperature regime on anthesis, pollen shedding and pollen viability. Means of 6 replications and 2 experiments each.

Temperature (°C)		Period between appearance of flag leaf, and start of pollen shedding (days)	Pollen shedding (days)	Pollen viability(%)	
day	night			start	end
27	22	5.3b [*]	2b	86a	83a
27	17	5.5b	3.3a	76b	56b
22	22	7.8a	3a	88a	87a
22	17	8.5a	3.5a	71b	45b

* Values in columns followed by the same letters are not significantly different ($p=0.05$) according to Duncan's new Multiple Range Test.

No difference in viability of pollen was found between spikes originating from main stems or from aerial tillers. Under field conditions at the Yotveta site, pollen viability generally decreased from the beginning of flowering in October until January by approximately 20% in spikes of N-74 of main stems and aerial tillers alike. This decrease of pollen viability was more than 30% in line N-51 (Fig. 4).

Fig. 4. Pollen viability of Napiergrass lines growing at Yotvata.

Synchronization of the flowering between napiergrass and pearl millet and aspects of seed production of hybrid Pennisetum.

The study of the synchronization of the flowering between the male (napiergrass) and the female (pearl millet) parents involved the investigation of the biology of flowering of each of the parents and the means by which flowering may be controlled under field conditions.

Four to five days were required to the individual inflorescence (spikes) of pearl millet to emerge above the sheaths of the flag leaf, and another three to five days to complete anthesis. The appearance of receptive stigmas preceded the shedding of pollen (in male fertile pearl millet plants). Even when spikes were not yet fully emerged, stigmas of exposed florets showed the typical curl splitting of their tops, presumed to be indicative of their receptivity to pollen. Usually the upper third part of the spike carries few spikelets only. After about 11 days from the start of the spike emergence, some two-thirds of its spikelets is pollen receptive leading to approximately 80% seed set.

Pearl millet 23A plants usually produced up to an average 13 flowering stems per plant (Fig. 5a) within approximately 16 days. Flowering of 1-2 secondary stems per main stem (the spikes were much

Fig. 5. Inflorescence emergence of (A) pearl millet 23A and (B) Napiergrass N-51

smaller) occurred after the completion of the flowering of the main stems.

Napiergrass plants produced a great number of spikes on main stems and on aerial tillers, the spikes of which also produced pollen (Fig. 5b). Two to three days elapsed between the extrusion of anthers and the start of anthesis. Pollen from the individual spikelet of napiergrass is shed during 2-3 days. The number of days during which spikes were produced by napiergrass was more than double that of pearl millet.

Weekly seedings of rows of pearl millet (23A) were carried out between established rows of napiergrass during August and September in three seasons at Yotvata. During 1982 and 1984 spike emergence of pearl millet occurred usually about 45 days after seeding irrespective of seeding date, whereas in 1983, apart from the first seeding, it exceeded 50 days and even reached 65 days, apparently caused by the cooler autumn season of that year (Fig. 6).

The time and the intensity of flowering of the different napiergrass lines showed some similarity between the years (Fig. 6).

All three lines started to flower at the end of October until mid-November. The intensity of flowering of line N-51 was very similar in 1982 and in 1984 but in 1983, it was about 65% less and took longer to reach its peak. Flowering intensity of N-20 was similar in 1983 and 1984 but in both years was less than in lines N-74 and N-51.

Fig. 6. The course of flowering of different Napiergrass lines and of Pearl millet 23A seeded at different dates at Yotvata.

Pearl millet

- Spike emergence
- Flowering
- ▲ Seeding

Napiergrass

- N51
- N74
- ▲—▲ N20

Synchronization between the flowering of both parents was found to occur when pearl millet was seeded on Sept. 5, 14, and 17 in 1982, 1983 and 1984 respectively. The period of ample pollen shedding of napiergrass during November coincided with the presence of ample numbers of respective stigmas of pearl millet when seeding of the latter was done during the first fortnight of September.

Although it was found that synchronization between the flowering of the male and the female parents can be achieved by adjusting the seeding date of pearl millet in September, it should be remembered that prevailing cool weather during autumn and winter period is not particularly favorable for seed formation and seed maturation. Thus, since line N-23 of napiergrass has shown in Yoyvata a greater requirement of short days for flowering than other lines, this line was selected for studying the possibility of hybrid seed production in the warmer spring season that is more favorable for seed set, development and maturity.

At weekly intervals from the end of January onwards, pearl millet 23A was seeded in rows either under plastic tunnels (40 cm. high), under plastic mulch or without any cover (control). The experimental treatments caused considerable increase of temperature in the upper layers of the soil and consequently, greatly accelerated seedling emergence and plant development, resulting in the advance of the onset of flowering compared to the control. On the average the emergence of spikes was about 55 days after seeding under tunnels

compared to 95 days in the control. The mulch treatment also caused an appreciable advancement of spike emergence especially in the early seedlings. During the early spring period, line N-23 of napiergrass slowly reached its peak of flowering at the beginning of April (Fig. 7a). From the results it was concluded that without technical means which lead to advancing the flowering of pearl millet in the spring it cannot be matched to the flowering of napiergrass.

In another experiment, artificial light from 60W filament lamps illuminated rows of N-23 napiergrass from a height of about 2m above the ground from the end of August till mid-December. Only continuous illumination was applied

The illumination (i.e. night break) prevented the flowering of napiergrass whereas the control plants (i.e. without night break) started flowering at the end of November with a peak in mid-January (Fig. 7b) . During mid-December the natural daylength is 10 h and inductive to flower initiation which was assumed to occur in mid-March followed by the flowering at the end of April with its peak in mid-May.

For napiergrass kept in the vegetative stage during winter by means of illumination, flowering in the spring is thought to be a practical technique that makes possible synchronization of flowering with spring seeded pearl millet without tunnels or mulch. This method, however, needs further exploration.

Fig. 7. The course of flowering of Napiergrass N-23 in 1982-3 (without illumination during the night) and in 1983-4 (with and without illumination) and flowering of Pearl millet 23A during the spring at different dates at Yotvata.

PERIODS OF
RECEPTIVE
STIGMA

... TUNNEL

— PLASTIC
COVER

= CONTROL

Δ Seeding

Pollination of pearl millet spikes was carried out during November 1982 in Yotvata by means of : (a) the release of pollen achieved by gently shaking flowering napiergrass stems over adjacently growing rows of flowering pearl millet; or (b) detaching pollen-carrying flower stems of napiergrass which were shaken above flowering pearl millet plants, and spikes were covered immediately after pollination with small bags. In both cases, care was taken to make sure that the pollen shed off the napiergrass was viable and that the pearl millet spikes exhibited receptive stigmas, (judged by split tops and yellow color). Fifty flowering pearl millet plants were used per method.

Seed set was observed to have taken place approximately 14 days after pollination. It was about 25% after applying method (a). However, seed set reached more than 80% after applying method (b). Usually the upper portion of the spike was void of seeds, but in the middle section of the spike seed set was often 100%.

Germination was approximately 85% in the mature seeds but not more than 40% in the shrivelled ones. The 1000-grain weight of mature seeds was approximately 4.5 g.

DESCRIPTION OF COOPERATION

In Israel there was cooperation between a scientist from the Department of Forage Crops and Range Management of the Agricultural Research Organization, the Volcani Center at Bet Dagan, and a scientist from the Department of Field and Vegetable Crops of the Faculty of Agriculture of the Hebrew University at Rehovot. Their research centered mainly around the physiology and agronomic aspects of the project. The cooperating U.S. scientists were from the USDA, Agricultural Research Center, Coastal Plain Experiment Station at Tifton Georgia, and they dealt mainly with the breeding and genetic aspects of the project. All plant material used for the studies in Israel was obtained from the U.S. investigators. Active contact was maintained between the investigators of both countries by correspondence through a constant exchange of information and material throughout the progress of the project.

One of the U.S. investigators (Dr. W.W. Hanna) visited Israel in the second year of the project. During this visit he obtained first-hand information on progress of the research, visited research installations and experimental fields throughout the country, including the Arava region where most of the research on seed production of hybrid Pennisetum was conducted. The visit was an excellent opportunity for mutual exchange of ideas and comment on research results, which were of great benefit to the progress of the research.

The Israeli investigators (Drs. T. Kipnis and A. Dovrat) visited the U.S., also in the second year of the project. Apart from visiting Tifton and becoming thoroughly acquainted with on-going research, they also visited research departments dealing with various aspects of the cultivation of warm-season grasses in Davis (Univ. of Calif.), San-Diego (State Univ.), Tucson (Univ. of Arizona) and Salt Lake City (Univ. of Utah). During the annual meeting of the American Society of Agronomy at Washington D.C., Dr. G.W. Burton of Tifton joined Drs. Hanna, Kipnis and Dovrat in discussions on the progress of the project and on planning of future research.

BENEFIT TO AGRICULTURE

1. Determination of growth potential prior to introduction of hybrid Pennisetum into a new region.

The growth potential and nutritive value of ^{the} hybrids is very sensitive to temperature. Phytotron studies formed the basis of a methodology that makes it possible to measure the optimum and critical temperatures for growth and to predict growth potential of Pennisetum hybrids for any temperature regime. The nutritive value of the grass can also be derived from this model. It is therefore possible to evaluate the chances of success of these hybrids and other tropical grasses as well in areas where they have not yet been introduced. This model can provide a guides for future breeding work of genotypes with wide thermal adaptation.

A descriptive mathematical model based on easily measured morphological traits in the field was developed for predicting the yield and quality of hybrid Pennisetum as a function of cutting frequency. This model can also be applied to grasses other than hybrid Pennisetum .

2. Vegetative propagation

A novel methods using aerial tillers was developed for the vegetative propagation of hybrid Pennisetum. This method proved to be more efficient and also enabled mechanical planting resulting is better and quicker field establishment than the conventional methods. The method seems to be of practical importance in regions where vegetative propagation of hybrid Pennisetum or its male parent napiergrass is the only way of field establishment.

3. Production of hybrid seed

Commercial seed production of hybrid Pennisetum has failed in the past. This was due to the lack of detailed information on the biology and thermo-photoperiodic requirements for flowering of the parent species, especially those of the male parent napiergrass. Suitable conditions for hybrid seed production exist in the south of Israel. After extensive experimentation, successful synchronization of flowering was achieved and it was shown that seed production is feasible in the Arava region of Israel. As a result, a new research project was initiated which aims at studying technologies for the commercial production of hybrid seed in Israel.

4. Breeding of short-day sensitive pearl millet and interspecific hybrids with napiergrass

The lines that were bred in conjunction with this project grow vegetatively for an extra month and a half towards the end of the growing season after other lines are already flowering. In the U.S, genes controlling short-day sensitivity in the pearl millet Sefa were transferred to Tift 23 and have been used to pollinate Tift 23DA to produce a later maturing cytoplasmic male sterile line. Preliminary data indicate that the newly developed lines can be used to advantage in both pearl millet hybrids and pearl millet x napiergrass interspecific hybrids to improve dry matter yield and or quality.

The pearl millet x napiergrass interspecific hybrids hold great potential for increased production of high quality forage under a wide range of climatic conditions.

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