Breeding for improved herbage and seed yield in Setaria sphacelata (Schumach.) Stapf and Hubbard ex Moss

A.J.P. van Wijk

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Promotoren: dr.ir. J. Sneep, hoogleraar in de leer van de plantenveredeling en
ir. J.G.P. Dirven, hoogleraar in de leer van het grasland.

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Abstract

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The simultaneous selection for yield of herbage and seed in Setaria sphacelata (Schumach.) Stapf and Hubbard ex Moss was studied, and the amount of variation present for each of these traits in relation to various plant characteristics was assessed in a spaced plant population and its open-pollinated progeny.

When comparing tillers at a similar stage of growth, a high in vitro digestibility was found for those tillers that originated from early-heading plants characterized by short length, light weight and narrow leaves. Comparisons of whole plants at 3 periods of regrowth revealed a negative correlation between in vitro digestibility and dry-matter yield. The variation found for in vitro digestibility was not repeated under sward conditions.

Plants with a high yield of clean seed were early-heading and large-sized. Of the three seed components studied, number of heads had the largest influence on seed yield. A high yield of clean seed did not necessarily mean a high yield of germinating seeds.

Simultaneous selection for herbage and seed yield could be carried out through selection for seed yield only, because of the high genotypic correlation between the two traits and the higher response expected from selection for seed yield. Selection indices should take into account time of head emergence and fresh weight of the plant at seed harvest time when selection was carried out after flowering. For selection before flowering, the index should include number, length and weight of tillers.

The testing of plants in a monoculture at wide spacing and in a sward of another species were compared.

When comparing lax, prostrate and erect growth habits, the erect-growing plant type proved to be the most productive and to have the highest competitive ability under the management applied.

The major research findings are summarized in a proposed breeding scheme.

Free descriptors: Setaria sphacelata, tropical grasses, in vitro digestibility, ageing, plant characteristics, herbage yield, seed components, seed yield, heritability, repeatability, single-plant evaluation, competition, index selection, selection response, breeding scheme.

This thesis will also be published as Agricultural Research Reports 900

Stellingen

1. Veredeling op een hogere verteerbaarheid in vitro zal in apomictische of klonaal vermeerderde grassoorten, die zich via stolonen of rizomen verspreiden, eerder tot succes leiden dan in panmictische, polvormende soorten.

G.W. Burton, R.H. Hart & R.S. Lowrey, 1967. Improving forage quality in Bermuda grass by breeding. Crop Sci. 7: 329-332.

2. Breese en Hayward zijn terecht van mening dat een nakomelingschapstoets in grassen teveel nadruk legt op de generatieve voortplanting in vergelijking met de vegetatieve voortplanting, daarbij dominantie en epistasie belangrijk makend. Zij houden echter geen rekening met de noodzaak van selectie via geslachtelijke cyclussen om van een landbouwkundig goed ras een commercieel succes te maken.

E.L. Breese & M.C. Hayward, 1972. The genetic basis of present breeding methods in forage crops. Euphytica 21: 324-336.

3. De creativiteit van de kweker wordt steeds verder teruggedrongen, omdat een groot deel van zijn tijd moet worden besteed aan het toenemend aantal administratieve handelingen en het meten van een groot aantal plantkenmerken voor rasbeschrijvingen, noodzakelijk bij het aanvragen van kwekersrecht voor nieuwe rassen en bij het opnemen en handhaven van rassen in aanbevelende rassenlijsten.

4. In gebieden waar de daglengte vrijwel constant is, is de bovengrondse biomassa op het tijdstip van zaadrijpheid van afzonderlijke planten van *Setaria sphacelata* een maat voor de groenvoeder - en zaadproduktiviteit van die planten.

Dit proefschrift.

5. Het vergelijken van kwaliteitskenmerken van grassoorten en -rassen zonder vermelding van vergelijkingsbasis en opbrengstniveau is zinloos.

Genbank - Informationsdienst (Braunschweig) Nr. 5, 1977.

6. Herhaalde recombinatie van genen bij kruisbevruchters die geselecteerd zijn onder bepaalde milieuomstandigheden, levert meer bruikbare variatie dan geïnduceerde mutaties.

J. Sneep, B.R. Murty & H.F. Utz, 1979. Plant Breeding Perspectives, Pudoc, Wageningen. p. 110-111.

7. De formule voor afname in heterozygotie door selectie in kleine populaties is een theoretisch gegeven zonder praktische toepasbaarheid.

D.S. Falconer, 1960. Introduction to quantitative genetics, Longman, London. p. 47-58.

8. Het kappen van schaduwbomen in theeplantages heeft naast teeltkundige effecten ook sociaal-economische gevolgen.

T. Visser, 1961. Interplanting in tea: 2 - The interaction of shade with fertilizer applications. Tea Quarterly 32: 113-128.

9. Naast infectie via geïnfecteerde bloeiwijzen van *Setaria* spp., wordt de schimmel *Tilletia echinosperma* via de stoppel en het stro overgedragen.

A.V. Bogdan, 1971. Notes on bunt disease of setaria grass. Kenya Farmer 183: 33.

10. Onder bepaalde omstandigheden kunnen partieel-resistente rassen van *Raphanus sativus* (bladramenas) dichtheidsverlagend werken op populaties van *Heterodera schachtii* (bietencystenaaltje).

11. Door hun continuïteit hebben zending en missie belangrijke voordelen boven ontwikkelingsprojecten die zijn opgezet door nationale, bilaterale en multilaterale instanties.

12. Deelname van lokale gemeenschappen in de bouw en het onderhoud van drinkwatervoorzieningen in ontwikkelingslanden is alleen zinvol als deze deelname zowel een delegatie van macht naar het lokale niveau inhoudt, alsmede een juiste verdeling van deze macht onder de verschillende klassen en categorieën in de gemeenschap.

C.A. van Wijk-Sybesma, 1979. Participation and education in community water supply and sanitation programmes. WHO IRC Techn. Paper 12.

13. De uitdrukking 'Laat er geen gras over groeien' dient, gezien de positie van Nederland als graszaadexporterend land, niet in letterlijke, doch in figuurlijke zin opgevat te worden.

Proefschrift A.J.P. van Wijk
Breeding for improved herbage and seed yield in Setaria spacelata (Schumach.) Stapf and Hubbard ex Moss.
Wageningen, 19 september 1980

'Asiyeuliza, hanalo ajifunzalo'

Curriculum vitae

The writer of this dissertation was born on 10 September 1946 in The Hague, received his secondary school education there at the Dalton Lyceum and took up his studies at the Agricultural University (Landbouwhogeschool) in Wageningen in 1964. He took his doctoral degree in plant breeding in 1971, with genetics and general phytopathology as subsidiary subjects. In the same year he went to Kenya with his wife under the terms of the Bilateral Cooperation Agreement between Kenya and the Netherlands to take part in a grass-breeding project at the National Research Station in Kitale.

His contract came to an end in 1977 and he returned to the Netherlands to join the Koninklijk Kweekbedrijf en Zaadhandel D.J. van der Have B.V. in Kapelle as a grass-breeder.

Acknowledgements

I wish to express my gratitude to my promotors prof.dr.ir. J. Sneep and prof.ir. J.G.P. Dirven: to the former for stimulating me to write this thesis and for his guidance and interest - to the latter for his many suggestions and continuous support in solving problems big and small.

I am greatly indebted to the Director of Research of the Ministry of Agriculture, Kenya, for making available to me the facilities at the National Agricultural Research Station in Kitale for this research and to the Dutch Ministry of Foreign Affairs for seconding me to the Kenya Government.

I gratefully acknowledge the help received from mr. M. Keuls, mr. P.J.S. Boon and dr.ir. E.W. Brascamp for statistical advice - the last named two also for making computer programs available.

My thanks are also due to ir. I. Bos who always answered my letters from Kenya on statistical problems promptly. He put forward many useful suggestions and read the manuscript carefully, as did dr.ir. G.E. van Dijk. Prof.dr.ir. J.H. van der Veen also commented on some sections.

I thank the staff of the Statistics Division of the Ministry of Finance and Planning in Nairobi for their unfailing patience with me when processing data on the computer.

I am grateful to mr. P.C.M. Groot who, as a student on a 6-month assigment, assisted me in making observations.

This study would have never been conducted and completed without the devotion of mr. Kefa Musia and mr. Zadock Akwisiela and their staff. Their friendship, commitment and skill are an indelible memory of Kenya. Mumefanya kazi nzuri sana na ninakumbuka jinzi tumeshirikiana pamoja kila siku. Utulivu, ujishugulishi na unyenyekevu wenu ulinivutia sana. Asante. I also wish to thank mr. P.K. Njoroge for the digestibility determinations of the many herbage samples.

I am very deeply indebted to dr.ir. J.G. Boonman who introduced me to the breeding of tropical grasses. Without his wide experience this study would never have been started. Our cooperation during those 6 years was unique and established a warm friendship between our families.

My special thanks go to my wife Christine and the children who created the happy atmosphere in which I could work and whose stimulation helped me to complete the present study on our return to the Netherlands.

I am grateful for the assistance and encouragement I received from D.J. van der Have B.V. to complete this thesis and I should, in particular, like to thank ir. D.J. Glas for his useful comments and ms. A.C.J. Dronkers, ms. D.A. Walraven-Hollestelle and ms. J.A. Sanderse-Yzerman for typing the manuscript

The efforts of the editorial staff of Pudoc in editing and publishing this study are gratefully acknowledged as are those of mr. A. Smith-Hardy for his assistance in dealing with textual difficulties.

Contents

1 Introduction

A first step in raising livestock productivity in tropical countries by improved grazing is the proper management of natural grasslands under grazing (e.g. regulation of grazing). Next comes the establishment of artificial pastures sown with local or introduced varieties. If these measures have been utilized to the full, a specific demand for better varieties, adapted to local conditions, will help to develop a breeding programme to cater for these requirements.

The demand for new varieties and the feasibility of breeding are in themselves not enough to justify the start of a breeding programme. Production units and outlets to market the developed material are essential. Regular quality control of the seed produced is another requisite.

Examples are rare of countries where these requirements for tropical grasses are met. At the Coastal Plain Station in Tifton, Georgia in the United States of America, G.W. Burton has directed a successful breeding programme on *Cynodon dactylon* (L.) Pers. (Bermuda grass) since 1945. The Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Queensland, Australia is involved in the breeding of many tropical pasture species, including *Brachiaria ruziziensis* Germain and Evrard (Congo signal grass), *Cenchrus ciliaris* L. (buffel grass), *Chloris gayana* Kunth (Rhodes grass), *Setaria sphacelata* (Schumach.) Stapf and Hubbard ex Moss (setaria) and *Sorghum almum* Parodi (Columbus grass). In these places, commercial enterprises are present to market the developed varieties, the quality of which is controlled by certification schemes. In Kenya, breeding started in 1954, and received a strong impetus from the establishment of the Kenya Seed Company in Kitale in 1956. This firm was set up by private grass-seed growers to produce and market selected varieties. Moreover, the Kenya Inspection Service for Seeds, established in 1970, ensured adequate seed quality. In Kenya the initiation of a grass-breeding programme clearly followed the developments outlined above. Apart from grassland agronomy, grassland research until 1960, aimed largely at the introduction of ecotypes and varieties, developed at home and neighbouring countries in order to obtain varieties superior to the current farmers' varieties. These consisted of seed harvested from natural stands of Rhodes grass or were material introduced from southern Africa, such as Rhodes grass and *Melinis minutiflora* Beauv. (Molasses grass) brought in by settler farmers. Eastern Africa, a centre of diversity for tropical grasses (Hartley & Williams, 1956) offered a great wealth of germ plasms. Over 4000 grasses and legumes originating from the local flora of East Africa were introduced between 1950 and 1960, mainly by A.V. Bogdan and R. Strange. Samples were also obtained from other African countries.

At the Grassland Research Station in Kitale these introductions were first screened in small observational plots, whereupon those with the best herbage productivity were further evaluated under grazing conditions (Bogdan, 1959). In addition to the two ley grass

species already under cultivation on a large scale in Kenya,(Rhodes grass and Molasses grass), setaria emerged as a productive species.

The evaluation work carried out in Kitale catered only for a small part of Kenya. About two-thirds of Kenya consists of semi-arid to arid land with an annual rainfall of less than 500 mm. These areas are situated at low altitudes and are too dry for cultivation. Only 12% of Kenya's acreage, situated at medium (1200-2000 m) and high (2000-3000 m) altitudes, can be referred to as high-potential areas thanks to adequate rainfall (more than 760 mm annually). In these areas, tropical ley grass species, such as Rhodes grass, Molasses grass, setaria and Congo signal grass can be grown. But at altitudes above 2250 m with an annual rainfall exceeding 1500 mm, even temperate-zone species like *Lolium perenne* L. (perennial ryegrass) and *Dactylis glomerata* L. (cocksfoot) can be grown. In a country where such extremes in climatic and ecological conditions occur, it was decided that pasture research should be carried out within a series of stations covering the major zones where 90% of the population lived. The Grassland Research Station in Kitale was responsible for research in the high-potential areas, where cash and food crops are grown and pastures developed as an integral part of mixed farming systems. The grass species selected in Kitale as productive were therefore especially suited to these high-potential areas.

Setaria, the grass species that was found to be as productive as Rhodes grass and Molasses grass, has been described under the species name *Setaria sphacelata* (Schumach.) Stapf and Hubbard ex Moss in "A revised list of Kenya grasses" by Bogdan (1958). This species name is generally accepted, though in Australia the same species is called *Setaria anceps* Stapf ex Massey, which is closely allied to *Setaria sphacelata* (Schumach.) Stapf and Hubbard ex Moss according to Bogdan (1977). These two species, together with some other *Setaria* species, form the *Setaria sphacelata* complex (Bogdan, 1961). Throughout the present study, however, *Setaria* is referred to as *Setaria sphacelata*, in conformity with the description given by Bogdan (1958).

Setaria is a tufted perennial with tall erect stems, which can grow to a height of 2 m. The inflorescence, a spike, is dense and cylindrical, usually 10-30 cm long, but sometimes longer. The spikelets are in clusters on short, branched penducles and are supported by bristles. Setaria phenotypically resembles the temperate grass *Phleum pratense* L. (timothy) and consequently is sometimes called golden timothy. The attractive features of this grass are its persistence and its tolerance to waterlogging, while a negative characteristic is its poor drought tolerance. Leaf diseases are not common on setaria in Kenya. A fungus disease called *Tilletia echinosperma* Ainsworth (Setaria bunt) can seriously damage the spikelets and affect seed yields adversely.

Deinum & Dirven (1976) found that the optimum day/night temperature for setaria was 29/23 ^{o}C, while the grass still grew very well at 23/18 ^{o}C. In Kenya, setaria can be cultivated at altitudes up to 2700 m, where mean temperatures are comparable with those of English summers (Bogdan, 1960). In Australia the setaria variety Narok was developed out of material collected in the Aberdare Mountains in Kenya at an altitude of 2200 m and this variety showed frost tolerance down to -3 ^{o}C.

Setaria therefore seems to be well suited to temperatures lower than those that normally occur in tropical areas and, in fact, the grass has been reported to be under cultivation in sub-tropical areas (Hacker & Jones, 1969). In the same paper of Hacker & Jones

setaria is also reported to occur naturally or to be under cultivation in several tropical countries, and to be widely adaptable, provided rainfall (or irrigation) is adequate (more than 800 mm annually).

Setaria has been reported as a cross-fertilising species (Gildenhuys, 1950) with a high degree of autoincompatibility.

Most tropical grass species are short-day plants (Humphreys, 1975) and setaria has also to be reckoned to this group. Boyce (1970), however, found it to be a quantitative long-day plant - his study was however based only on a few plants.

As is evident from what has already been mentioned, setaria is mostly used as a ley grass in the high-potential areas. It plays an important part in crop rotation with maize and cereals mainly in mixed farming enterprises. The best results have been obtained with early sowing at the beginning of the raining season. Undersowing to maize or cereals is not recommended. Because of its tufted growth habit, establishment is not as easy as with the spreading Rhodes grass, but once the grass has been established, it is much more persistent than Rhodes grass.

Out of the 106 local and introduced forms of setaria and *Setaria splendida* Stapf (giant setaria) made and examined by Bogdan and Strange (Bogdan, 1960) 12 introductions of setaria were found to be highly productive and of good herbage quality, and of these an ecotype from the Nandi district in Kenya proved to be the most outstanding (Bogdan, 1959). This ecotype was introduced by D.C. Edwards in 1935 from the Baraton Veterinary Centre in the Nandi area. The Nandi ecotype was planted in a plot of 100 square meters in Kabete near Nairobi for the bulking up of seed.

From this seed a plot of 400 square meters was established in which the ecotype was maintained. The grass was brought to Kitale in 1952 for comparison with other setaria introductions. As soon as the production characteristics of the Nandi ecotype were known, the grass was multiplied vegetatively to establish seed production fields. Seed became available to farmers in 1957 under the varietal name Nandi setaria.

From a study of the Nandi population in 1953 it became apparent that great variation occurred in this ecotype (Bogdan, 1959) and that there was wide scope for further selection. A breeding programme was then initiated.

When defining breeding objectives for tropical grasses, it should be realised that most tropical grasses are short-day plants. As length of day in tropical areas varies from nil at the equator to slight elsewhere flowering heads are produced during the entire growing season. This contrasts with many temperate, perennial grass species which require a low temperature followed by a long day for inflorescence initiation. Independent of the stem elongation during inflorescence development, tropical grasses show stem elongation in vegetative tillers as well, and this is also a continuous process throughout the growing season. In temperate grasses, stem elongation coincides with inflorescence development. Tropical grasses therefore are more stemmy than temperate grasses, and this could be one of the factors explaining the lower nutritive value of tropical grasses.

Because of the processes described above, it was no wonder that Bogdan (1959) considered leafiness and late flowering, combined with high vigour, as the major breeding objectives. The breeding programme that was started in 1954 with the material collected by D.C. Edwards in 1935 has been summarized in Table 1. During 3 generations 40-50 of the

Table 1. The development of Nandi I, Nandi II and Nandi III.

Year	Activity	Resulting variety
1935	Collection of Nandi ecotype	
1935-1952	Maintenance of Nandi ecotype in Kabete	
1952-1954	Evaluation of Nandi ecotype with other setaria introductions in Kitale	
1957	Commercial release of Nandi ecotype :	Nandi setaria
1954-1959	Recurrent mass selection during 3 generations in the Nandi ecotype :	Nandi II
1961	Commercial release of Nandi II Nandi setaria renamed as :	Nandi I
1959-1963	Half-sib selection from Nandi II :	Nandi III
1965	Commercial release of Nandi III	

best performing plants were selected out of 1000-1200 spaced plants of the Nandi ecotype (Bogdan, 1965). The selected plants were planted from splits to form an isolated polycross. The polycross seed from the third selection cycle was bulked to form a variety, called Nandi II, which was commercially released in 1961. The original Nandi ecotype, Nandi setaria, was subsequently renamed Nandi I. Selection was continued and 1000 spaced plants of Nandi II were scored for vigour, leafiness, regrowth and time of heading during 1959, 1960 and 1961. 25 outstanding plants were selected. The half-sibs of these 25 plants were tested and 16 of their parent plants were selected, according to performance, for a final polycross. The bulked seed of this polycross was released under the varietal name Nandi III in 1965.

The development of Nandi II out of the original Nandi ecotype caused a loss of 1% heterozygotes per generation of selection while, for the development of Nandi III out of Nandi II, the loss of heterozygotism amounted to 3%. These losses might have caused a genetical narrowing of the characteristics which were not under selection pressure.

No variety trials preceeded the release of the new varieties and, apart from the fact that Nandi III was about 1-3 weeks later in flowering than Nandi I, with Nandi II intermediate, other varietal characteristics were not known. As early-heading varieties were thought to be of inferior nutritive value, the multiplication of basic seed of Nandi I was discontinued in 1967. In the Annual Report of the Ministry of Agriculture for 1968, however, it was reported (Thairu, 1971) that Nandi I outyielded Nandi III in seed production with 140 and 190% in 1967 and 1968, respectively. Boonman (1971b) found that Nandi I had fewer but heavier tillers than Nandi III and Nandi III maintained a larger proportion of non-heading tillers throughout the heading period (Table 2 - the abbreviations used are explained in Appendix 1). The superiority of Nandi I over Nandi III in herbage and seed production was reported by Boonman & Van Wijk (1973) and Van Wijk (1976). The va-

Table 2. Characteristics of Nandi I, Nandi II and Nandi III. (After Boonman, 1971b, 1972c, 1973a and Boonman & Van Wijk, 1973).

	Period of observation	Nandi I	Nandi II	Nandi III
Sequence in IHE (weeks)	1968-1971	1	2-3	3-4
Maximum number of tillers per m^2 in the year of establishment	1968	620		800
Maximum number of tillers per m^2 in the 2nd year after establishment	1969	1400		1920
Weight per tiller (mg) at IHE in the year of establishment	1968	760		390
Weight per tiller (mg) at IHE in the 2nd year after establishment	1969	260		220
Number of heads per m^2 at optimum seed harvest time	1968-1971	250		125
Maximum percentage heading tillers	1969	25		9
Culm length at optimum seed harvest time (cm)	1969	150		135
1000-grain weight (mg) at optimum seed harvest time	1968-1971	420		420
PGS yield per crop (kg/ha) at optimum seed harvest time	1968-1971	32	22	15
PGS yield per head (mg)	1968-1971	12.8		12.0

rietal differences in seed production will be discussed in Chapter 3.

As seed production is already low in cultivated, tropical grasses compared to temperate grasses, it was clear that the seed production of Nandi II and Nandi III compared unfavourably in economic terms with that of Nandi I. In view of this, and because of its herbage productivity, Nandi I was taken back into production in 1972 and became the most important variety of setaria produced commercially. Production of Nandi III was stopped in 1970 and Nandi II in 1975. A 4-year average (1973-1977) of seed sales of Nandi I by the Kenya Seed Company, Kitale (R.G. Combes, pers. comm.) shows that 23 tons had been sold annually, 58% of which was exported (mainly to Brazil). It should be realised that only 1 kg of pure germinating seeds is required for the establishment of a pasture of 1 hectare. 86% of the seed sales within Kenya were in large units, while the remaining 14% was sold in 1 kg packets. These small units are becoming more popular every year among Kenya's small-scale farmers: 1 kg of seed, with a germination percentage of 25-30%, is sufficient to establish a pasture of 0.25 hectare.

Apart from the varietal differences and the inherent low seed-yielding ability of cultivated tropical grasses, crop-physiological difficulties were among the causes of the short supply of seed in the sixties, which was the major obstacle to increase the area under pasture in Kenya and neighbouring countries. Boonman (1973b) therefore developed crop-husbandry techniques which increased seed yields considerably. Because of the higher yields, seed prices could be maintained over a long period when costs of other inputs were rising continuously, so that seed could even be exported, as stated above. It was realised, however, that if the varieties in commercial production were less variable, seed yields could be even higher. A new breeding programme was therefore initiated in 1971 at the Kitale National Agricultural Research Station in which the Grassland Research Station had been incorporated in 1963. The new programme aimed at the development of uniform va-

rieties with a higher herbage and seed production than the existing ones.

In the new breeding programme old seed fields of existing varieties of known name and history were chosen as the source population from which breeding could be started. As low seed production was the main limiting factor of the Kitale varieties, it was thought that material taken from seed-production fields would have undergone a shift towards better seed-yielding characteristics, while material from old pastures would be poor in seed production. Vegetative material was then collected at random from old seed production fields and some 4000 plants from both Nandi I and Nandi II were planted one per square meter (Boonman, 1971a). Concurrently a similar programme was carried out with 3 varieties of Rhodes grass. The main reason for establishing spaced-plant populations was to stabilize the existing varieties, as varieties were multiplied from generation to generation up till 1968, resulting in a genetic shift, given the wide intra-varietal variation present.

Intra-varietal variation was studied in these populations and the spaced-plant populations also served as a source of pre-basic seed, which was passed to the Kenya Seed Company for further multiplication to basic seed (by this company) and certified seed (by contract farmers).

The breeding programme, in which growth vigour and matching heading times were the major objectives, resulted in the variety Nasiwa, which is 1 week later than Nandi I. The variety was taken into commercial production: 20 ha of basic seed was sown in 1977 and seed therefore became available to farmers in the 1978 season. Nasiwa produced 96 and 47 kg of pure germinating seeds per ha in the first and second crop of 1977, respectivily, while yields from Nandi I rarely exceeded 30 kg of pure germinating seeds per ha per crop.

Besides the breeding programme in setaria, a study was conducted concurrently in this species to gain more insight into the plant characteristics determining herbage and seed production, and to define the phenotypic characters upon which selection had to be based. The results are reported here.

The research consisted of 2 parts:

- a study of various plant characteristics of 121 plants, randomly chosen out of the spaced-plant population of Nandi I and their open-pollinated progenies, from which selection indices were composed to define the characteristics determining herbage and seed yield.
- a study of the effect of ageing on digestibility and the relationship between herbage quality and quantity, a comparison of evaluating plant material as spaced plants in monoculture and mixed culture and a yield trial of plants with different growth habits in monoculture and mixed cultures.

The trials that will be reported were conducted between 1973 and 1977 at the National Agricultural Research Station in Kitale, which is situated at an altitude of nearly 1900 m at 1° North latitude. Because of the latitude, daylengths are virtually constant throughout the year. The yearly maximum and minimum temperatures (averages of 16 years) are 25.4 and 11.2 °C, respectively (Pratt & Gwynne, 1977). In Table 3 the official rainfall figures are given for the years that the trials were conducted.

The rainy season usually starts in early April and continues till late in November. From December till April it is usually dry. Most of the rain falls between April and September. The average annual rainfall (over 16 years) is 1242 mm (Pratt & Gwynne, 1977).

Table 3. Official rainfall figures (mm) for Kitale.

	1973	1974	1975	1976	1977
January	27	13	-	5	85
February	109	6	8	32	36
March	5	132	59	24	39
April	45	109	135	99	184
May	206	147	211	205	169
June	94	76	168	67	223
July	35	172	115	181	104
August	281	123	132	97	148
September	126	132	160	116	45
October	23	78	109	59	155
November	88	21	38	31	180
December	3	34	27	34	68
Total	1042	1043	1162	950	1436

Maximum mean monthly temperatures vary from 25.7-27.8 °C in the dry season and during the rainy season they vary from 22.9 °C (July) to 26.0 °C (April) (averages of 16 years). Minimum temperatures vary to a smaller extent during the year: from 10.0 °C in January to 12.7 °C in April. The soil at the National Agricultural Research Station has been described as a dark reddish-brown clay, which overlies a dark-red clay (Mickieka & Oswaggo, 1971). The soil is deep and well drained, its pH_{water} is 5.5. The soil is deficient in phosphorus and nitrogen.

Growth rate of Setaria is highest during the first weeks of the rains after the dry season (Sheldrick & Thairu, 1975). The majority of plants produce heads within a short time during this period. Later-heading plants produce heads over a longer period owing to the strong competition of the early-heading plants. With the pattern of rainfall in Kitale two seed crops a year can be grown, but because of the lower rainfall during the second crop, heading is more gradual and growth rates are lower.

An explanation of the abbreviations used in the text is given in Appendix 1.

2 Variation of plant characteristics and its relationships with in vitro digestibility and herbage yield

2.1 INTRODUCTION

Properly managed, pastures of tropical cultivated grasses produce high yields of dry matter which can amount to 45 tons per ha according to Dirven (1970). Milk production from animals fed on these grasses, however, compares unfavourably with that from cows grazing temperate grasses. Climatic conditions, the genetic conditions of the animal breeds and the nutritive value of the roughage are the main causes of this difference. As climate is an unchangeable factor, animal production can only be improved by altering the last two factors. Zootechnical measures will be excluded (e.g. the introduction of exotic breeds and the breeding of animals) and only the nutritive value of the roughage will be considered here.

The nutritive value of a grass can be defined as the product of voluntary intake, digestibility and the efficiency of utilization of the digested nutrients by the ruminant (Raymond, 1966). In tropical grasses the first two factors are primarily responsible for the low levels of milk production by dairy cattle (Stobbs, 1971).

Concentrate supplementation will improve the nutritive value of grass diets, but the utilization of grasses bred for high-intake characteristics and high digestibility will reduce the animals' need for concentrates and consequently the costs. Moreover, concentrates compete with the human-consumption needs. For this reason there might be great benefits in the long run by breeding for quality in grasses. Improving dry-matter production will simultaneously increase the carrying capacity of a pasture per unit area.

Intake and digestibility can be determined by feeding trials. In these trials, however, selection by the animals of the roughage offered is greatly reduced and differences may occur between the results obtained in feeding trials and in outdoor grazing experiments. Moreover, in a breeding programme, large numbers of genotypes have to be screened, often on a single-plant basis, which makes these trials inapplicable. Laboratory techniques needing only small amounts of material are therefore required.

Various methods to determine intake in vitro have been developed, which had good correlations with in vivo, but were found to vary considerably in their precision of prediction (Jones et al., 1974). Digestibility can be measured more accurately and the 2-stage technique of Tilley & Terry (1963) which combines precision and rapidity seems to be the most promising. Jones (1975) therefore suggested that breeding programmes for nutritive value should initially aim at improving digestibility. The high-digestibility strains once developed could then be further screened for voluntary intake. However, marked differences in voluntary intake between varieties within a species at similar levels of digestibility have been reported both for temperate and tropical grasses (Walters, 1974; Jones et al., 1974; Minson, 1977). There is no consensus of opinion as to the plant or chemical fac-

tor which should be held responsible for these differences and voluntary intake as measured by laboratory procedures, will still be an elusive characteristic in grass breeding. Minson (1977) wisely advised study of the physical plant factors (e.g. leaf percentage, hairiness of leaves and stems, silica teeth along leaf blades) rather than chemical analyses, as a means of determining what controls intake.

Any comparison on digestibility on plants or varieties with different growth rhythms is bound to reflect the method used for evaluating the material owing to the correlation between ageing and maturity. Determinations on grasses cut at the same date imply that material of the same age, but of different maturity has been looked at, whereas samples of material from grasses of the same maturity, as expressed by a defined growth stage, will in fact be of different ages.

The correlation between ageing and maturity is stronger in temperate grasses than in tropical grasses as stem elongation in the former clearly coincides with the stage of inflorescence development, while in tropical grasses stem elongation is a continuous process. Inflorescence development in tropical grasses therefore does not change the proportion of stems so drastically as it does in temperate grasses.

Walters et al. (1967) attributed the observed variation in digestibility of some temperate grasses largely to differences in growth stage. When compared at the same maturity, early-heading varieties, being younger, were of higher digestibility than late-heading varieties (Dent & Aldrich, 1963). On a single-plant basis within a variety of cocksfoot, early-heading plants were more digestible than late-heading plants compared at the same morphological stage (Mowat et al., 1965). In order to compare varieties, independent of growth stage, Green et al. (1971) studied yield and quality of various grasses in their development up to flowering by cutting undisturbed regrowth at 10-day intervals. Varieties can then be compared at any given yield of dry matter or level of digestibility.

Heritability estimates for in vitro digestibility have been made for various grasses, the results of which are presented in Table 4. For each grass the base of comparison (i.e. comparing plants or families at a given time irrespective of the growth stage, or comparing plants or families when a defined morphological development has been reached) and the type of genetical material have been mentioned. Generally speaking, heritabilities in the wide and the narrow senses were high and thus mass selection seems to be applicable as a breeding method for improving digestibility. In view of the high heritability values it should be emphasized that accuracy in estimating heritability is low and that heritability values are bound to include large standard errors.

Apart from the heritability estimated by Coulman & Knowles (1974), the heritabilities in the narrow sense have been estimated as twice the regression of the offspring means on the parent means, which may lead to values greater than 1 as has been the case with Carlson et al. (1969) and Ross et al. (1970). Values larger than 1 are acceptable so long as standard errors are reported as well, which was not the case with Ross et al. (1970).

Coulman & Knowles (1974) estimated the heritability in the narrow sense as twice the correlation between the parent and the offspring means. Carlson et al. (1969) reported a highly significant clone × year interaction in their heritability calculations for di-

Table 4. Heritability estimations for in vitro digestibility of whole plants.

Species	Heritability		Basis of comparison and type of material	Author(s)
	Wide sense	Narrow sense		
Agropyron cristatum L. (crested wheatgrass) & *A. cristatum* x *Agropyron desertorum* (Fisch ex Link) Schult. (fairway wheatgrass)		0.36 - 0.76	Growth stage Parent/offspring	Coulman & Knowles, 1974
Andropogon gerardi Vitman (big bluestem grass)		0.72	Growth stage Half-sibs	Ross et al., 1975
Bromus inermis Leyss (smooth bromegrass)	0.73		Growth stage Clones	Christie & Mowat, 1968
Bromus inermis Leyss (smooth bromegrass)		1.06	Growth stage Parent/offspring	Ross et al., 1970
Bromes inermis Leyss (smooth bromegrass)	0.86	0.64 & 0.67	Time basis Diallel	Sleper et al., 1973
Chloris gayana Kunth (Rhodes grass)	0.19 & 0.49		Time basis Half-sibs	Sleper, 1974
Chloris gayana Kunth (Rhodes grass)	0.15		Time basis Clones	Boonman, 1978b
Cynodon dactylon (L.) Pers (Bermuda grass)	0.27 - 0.78		Time basis Clones	Burton & Monson, 1972
Dactylis glomerata L. (cocksfoot)		0.53	Time basis Parent/offspring	Cooper et al., 1962
Dactylis glomerata L. (cocksfoot)	0.73		Growth stage Clones	Christie & Mowat, 1968
Lolium perenne L. (perennial ryegrass)		0.64 & 0.06	Time basis Diallel	Rogers & Thomson, 1970
Phalaris arundinacea L. (reed canary-grass)	0.21 - 0.51	0.30 - 1.31	Time basis Clones & parent/offspring	Carlson et al., 1969
Phalaris arundinacea L. (reed canary-grass)	0.78	0.71	Time basis Clones & parent/offspring	Hovin et al., 1974
Phalaris tuberosa L. (bulb canary-grass)	0.54 & 0.77		Time basis Clones	Clements, 1973
Phalaris tuberosa L. (bulb canary-grass)		0.60	Time basis Full-sibs within half-sibs	Oram et al., 1974

gestibility and therefore advocated that selection should be based on the mean performance in replicated trials conducted for at least 2 years.

The two heritability values obtained by Rogers & Thomson (1970) were estimated from the same experiment during two consecutive years. The higher variance for general combining ability relative to the specific combining ability variance in the first year when h_n^2 amounted to 0.64, decreased in the second year, resulting in $h_n^2 = 0.06$. It was suggested that the more intensive interplant competition in the second year could account for this

change, but this was not further substantiated. Care should therefore be taken not to rely on heritability estimates made on the basis of one single year alone.

Some of the heritabilities in the wide sense were based on plant or plot means rather than on individual plant or plot values, such as those obtained by Sleper et al. (1973), Hovin et al. (1974) and Sleper (1974). These heritabilities, calculated from the components of variance through clonal or family replication are dependent on the number of replicates: the higher the number of replicates the higher the estimate of heritability. Heritabilities based on plant or plot means therefore give too high an estimate if individuals are the basis of selection.

The two values estimated by Sleper (1974) refer to 2 weeks' and 6 weeks' regrowth. At 2 weeks' regrowth the genetic variability for digestibility was still low. Variation between plants was greater at a later harvest date. The range in values obtained by Burton & Monson (1972) originated from different harvest times and years. The heritability estimates reported by Clements (1973) refer to different growth stages of the same material. Boonman (1978b) reported low heritability in the wide sense but the material from which the estimated heritability was obtained was selected for matching heading dates, thus the amount of genetic variation present had been narrowed.

The results on heritability estimates as presented in Table 4 were mostly based on variability studies within or between populations, aiming at intra- or inter-populational mass selection. Another approach to digestibility improvement is the hybridization of plants, species or genera to introduce plant characteristics which influence digestibility. Breeding for digestibility in this way has been succesful in the case of Bermuda grass, which is a vegetatively propagated, spreading species.

Because of this latter characteristic, a plant of high digestibility, once developed can be maintained by vegetative multiplication and so will the variety, descending as it does from one clone. The fixation of the desired characteristic, i.e. the high digestibility, can therefore be easily done. The highly digestible Bermuda grass variety Coastcross was obtained by hybridizing the variety Coastal Bermuda with a highly digestible Bermuda grass introduced from Kenya and by selecting the most digestible hybrid at different periods of regrowth (Burton et al., 1967). The average dry-matter digestibility of Coastal Bermuda grass and the Coastcross hybrid over a 4-years period, cut at regular intervals, amounted to 53.5 and 60.1%, respectively. Utley et al. (1974) found that steers grazing Coastal Bermuda grass and Coastcross displayed a live-weight gain of 372 and 527 kg per ha per grazing season (lasting spring and summer), respectively. The values were calculated from average values for stocking rate, days of grazing and average daily gains during a 4-year period.

Species-crossing as a means of improving digestibility has been applied in cocksfoot (Breese & Davies, 1975). The cocksfoot variety S 37 was hybridized with *Dactylis marina* Borrill, which is characterized by the absence of silicified teeth on the leaves, highly papillose epidermis cells, superior digestibility and a low growth rate. The aim was to combine these characteristics with the good herbage and seed yield of S 37. Selection was made among 210 spaced F_1 plants, 12 of which were ultimately polycrossed. The progenies were tested in swards, the whole-plant digestibility being determined on 7 dates. Apart from the first cut, digestibility of the twelve F_2 families was 1-8% digestibility units

higher than the control variety S 37. Herbage yield data were not presented.

Work has also been done on intergeneric crossing between *Lolium multiflorum* Lam. (Italian ryegrass) or perennial ryegrass and *Festuca arundinacea* Schreb. (tall fescue), which aimed at the improvement of the digestibility and the intake characteristics of tall fescue. Cytological instability and difficulties of seed production still cause problems in many such breeding programmes.

What is of interest is the extent to which the observed or created variability can be attributed to inherent differences in digestibility and how much to variability of other plant characteristics. Once these variabilities have been separated and defined, initial screening in large plant populations will be greatly facilitated.

Part of the variability for digestibility is not of genetic origin, but must be contributed to environmental effects. The various heritability values given in Table 4 already pointed to the variables affecting digestibility, such as year effect and length of regrowth. Numerous studies have been carried out to investigate the effect of temperature, light intensity, fertilizer application, water stress and cutting management on digestibility. Part of these studies have been summarized by Deinum (1974).

In grass breeding, dry-matter yield is a major breeding objective which is directly influenced by the tolerance to biotic and abiotic factors affecting the persistence of the sward. When breeding for digestibility these characteristics should be held at the level at least or even simultaneously improved.

The present studies were designed to assess the variability for in vitro digestibility and dry-matter yield within the variety Nandi I and other varieties of setaria and to determine the relationship between these characteristics and various other plant properties. For the assessment of intra-varietal variation 121 spaced plants were compared at a similar growth stage (Section 2.2) and at equal times of regrowth (Section 2.3). The inter-varietal comparison was made by harvesting undisturbed regrowth at 2-weeks intervals (Section 2.4).

2.2 INTRA-VARIETAL COMPARISONS MADE AT THE SAME GROWTH STAGE ON 15 TILLERS

2.2.1 Material and methods

The spaced plant population of Nandi I, as mentioned in the first chapter was established in April 1970 (Boonman, 1971a). In 1973 a block of 11 x 11 plants was chosen at random within the population of 4000 plants of Nandi I. Between 1970 and 1973, six seed crops (in 1972 and 1973 two seed crops per annum) were taken from the 4000 plants during which period the plants recieved 500 kg of nitrogen per hectare.

The 121 plants were propagated vegatively in polyethylene bags on 12 November 1973. One week later the plants were transferred to the field and planted as single plants in an 11 x 11 triple lattice, one per square meter. At time of planting the plants received 40 kg of phosphate per hectare. Guard rows were planted round each replicate. The plants were irrigated throughout their establishment period. Dead plants (10% in each replicate) were replaced by spare plants 1 month after planting. On 20 March 1974 the plants were top-dressed with 40 kg of nitrogen per hectare, followed by a cleaning cut at a height of

10 cm on 11 April. On 10 September 1974 all plants were cut back (at a height of 15 cm) and top-dressed with 100 kg of nitrogen per ha, as were subsequent crops on 17 April 1975 and 5 August 1975.

The cutting height was that at which it could conveniently be done with sickles. In April 1974 the cutting height was lower than in September 1974 because of the younger material then present: when the plants became older, dead material was accumulated in the stubble, which brought the level of cutting to 15 cm in September. This cutting height could be maintained throughout the life of the plants without encountering practical problems.

The following characteristics, as defined in Appendix 1, were taken of the three crops:

- number of tillers per plant;
- time of head emergence per plant;
- tiller angle of the plant;
- average length of 15 tillers;
- total number of leaves of 15 tillers;
- average leaf width of 15 tillers;
- average leaf length of 15 tillers;
- average stem diameter of 15 tillers (only measured in the 2 crops of 1975);
- dry weight of 15 tillers;
- fresh weight of the whole plant at seed harvest.

Leaf width, leaf length and stem diameter were measured on tillers that were still attached to the plant, while tiller length, leaf number and tiller dry weight were determined from cut (at a height of 15 cm) tillers. In determining the fresh weight at seed harvest, the weight of the 15 tillers was excluded. The characterictics were chosen as described below. The structure of the vegetative grass canopy is determined by tiller number, tiller angle, leaf size (particular leaf length), leaf angle and leaf rigidity (Rhodes, 1973a). In an earlier study with the 121 plants (data not presented) leaf angle and leaf rigidity proved to be of minor importance in determining digestibility, while their measurement was very cumbersome. Moreover, these characteristics were most variable under field conditions. The other three canopy characteristics, tiller number, tiller angle and leaf length were thought to affect the yield of the plant, while leaf length was held to be a characteristic with possibly a strong influence on digestibility. Time of head emergence was an important property because of the much reported relationship between age and digestibility. Tiller length, leaf number, leaf width and stem diameter have been reported to affect digestibility and were for that reason included in the series of measurements. The dry weight of the 15 tillers was included to investigate the relationship between dry-matter yield and D_{vitro}. Boonman & Van Wijk (1973) found that growth vigour was an important factor determining time of head emergence. But as growth vigour, observed on a relative scale, was subjective, it was thought that the total bulk of the plant at seed harvest would provide information about the growth vigour of the plant at its time of head emergence.

The 15 dried tillers whose weight was found, were milled. As it was too laborious to determine D_{vitro} of all 121 plants in the different harvests per replicate, 50 randomly

chosen plants were measured for D_{vitro} per replicate and per harvest. The remaining 71 plants of 3 replicates and 3 harvest were bulked per entry - the aggregate sample was analysed for D_{vitro}.

The measurements taken in 1974 and 1975 were summed per entry and per replicate (for D_{vitro} only 50 plants) and analyses of variance of all characteristics and of covariance between the characteristics (except D_{vitro}) were carried out according to the following model:

$$Y_{ijk} = \mu + r_i + b_{j:i} + P_k + e_{ijk}$$

in which

Y_{ijk} = observation of plant k in block j in replicate i
μ = overall mean
r_i = fixed replicate effect; i = 1,2,3
$b_{j:i}$ = fixed block effect within replicate i; j = 1,2 11
P_k = random plant effect; k = 1,2 ... 121
e_{ijk} = random error

The analysis of variance in Table 5 was calculated with the least squares analysis of Harvey (1976). The coefficient of the genotypic variance component was 2.75. The estimates of the genotypic variance (s^2_g) and that of the phenotypic variance (s^2_{ph}) were calculated from Table 5 as follows:

$$s^2_g = \frac{MSC - MSE}{2.75} \quad (b = 11,\ r = 3)$$

$$s^2_{ph} = MSE + s^2_g$$

For the analysis of covariance the same model and the same analysis as in Table 5 were applied, but, instead of the mean squares, the mean cross-products between the various

Table 5. Analysis of variance of n clones in k blocks within r replicates. r = number of replicates; b = square root of number of clones = number of blocks; n = number of clones; σ^2_e = error component of variance; σ^2_g = genotypic component of variance between clones.

Source	Degrees of freedom	Mean squares	Expected mean squares
Replicates	r-1	MSR	
Blocks within replicates	r(b-1)	MSB	
Between clones corrected for blocks	n-1	MSC	$\sigma^2_e + \frac{b}{b+1} r \sigma^2_g$
Error	(b-1)(rb-b-a)	MSE	σ^2_e
Total minus correction term	rn-1		

characteristics were calculated. The genotypic and phenotypic covariances between the characteristics A and B, $s_{g,AB}$ and $s_{ph,AB}$, respectively were estimated from the mean cross-products as in the analysis of variance.

The genotypic correlation coefficient between characteristics A and B ($r_{g,AB}$) and the phenotypic correlation coefficient between A and B ($r_{ph,AB}$) were defined as:

$$r_{g,AB} = \frac{s_{g,AB}}{\sqrt{s^2_{g,A} \times s^2_{g,B}}}$$

$$r_{ph,AB} = \frac{s_{ph,AB}}{\sqrt{s^2_{ph,A} \times s^2_{ph,B}}}$$

in which $s^2_{g,A}$, $s^2_{g,B}$, $s^2_{ph,A}$ and $s^2_{ph,B}$ are the genotypic and phenotypic variances of A and B, respectively.

In the analysis of variance and covariance, plants were corrected for blocks, except for D_{vitro} and its covariances, which were tested as being derived from plants in a randomised block design.

Heritabilities in the wide sense on an individual-plant basis were calculated as

$$h^2_w = \frac{s^2_g}{s^2_{ph}}$$

The repeatability of each characteristic over 3 harvests was determined from the totals of the 3 replicates per plant per harvest according to the analysis of variance in Table 6. The estimates of the variance between plants (s^2_b) and within plants (s^2_w) were calculated from Table 6 as follows:

Table 6. Analysis of variance of n clones in r repetitions of observations. n = number of clones; r = repetition of observations.

Source	Degrees of freedom	Mean squares	Expected mean squares
Between clones	n-1	MSB	$\sigma^2_w + r\,\sigma^2_b$
Within clones	n(r-1)	MSW	σ^2_w
Total minus correction term	rn-1		

$$s_b^2 = \frac{MSB - MSW}{3} \quad (r = 3)$$

$$s_w^2 = MSW$$

The repeatability was defined as

$$R = \frac{s_b^2}{s_b^2 + s_w^2}$$

The means of the 3 harvests corrected for block effects for all characteristics (except D_{vitro}) were used for a multiple regression analysis with D_{vitro} of 121 plants as the dependent variable according to the method of Daniel & Wood (1971) as described in Appendix 2. The subset equation finally selected was subjected to a path analysis according to Dewey & Lu (1959).

2.2.2 Results

Table 7 gives the range and the coefficients of variation of the measured characteristics, averaged over 3 replicates and 3 harvests. From this table the large phenotypic variation within the Nandi I variety is evident. Head emergence was spread over a period of 7 weeks and various types of plant were found to occur. The range in D_{vitro} was large (individual observations varied from 47.9-64.2), but the extremes were rare, as can be seen from the small coefficient of variation.

Differences between plants were significant ($P < 0.01$) for all characteristics, so that selection at a comparable growth stage for one of them seems feasible. The significance of the block effects varied from one characteristic to the other.

Genotypic and phenotypic correlation coefficients between the measured characteristics are shown in Table 8. The relationships with D_{vitro} were based on 50 plants. A stri-

Table 7. Ranges and coefficients of variation (% CV) of the measured characteristics (means of 3 replicates of 3 harvests) of 121 plants.

Characteristic	Range	% CV
Tiller number	109-749	31.0
Time of head emergence (week)	1-7	30.8
Tiller angle	1.41-2.11	8.1
Tiller length (cm)	43-75	6.8
Leaf number of 15 tillers	61-99	9.0
Leaf width (mm)	7-11	8.6
Leaf length (cm)	17-26	10.1
Stem diameter (mm)	2.6-3.8	6.8
Tiller weight of 15 tillers (g)	11-30	19.7
Fresh weight of the plant (kg)	0.5-3.1	30.7
D_{vitro} (%)	50.7-60.7	3.4

Table 8. Genotypic and phenotypic correlation coefficients between the measured characteristics.

	Tiller number	Time of head emergence	Tiller angle	Tiller length	Leaf number	Leaf width	Leaf length	Stem diameter	Tiller weight	Fresh weight of the plant	D_{vitro}[2]
Tiller number	-	-0.169[1] -0.280	-0.295 -0.173	0.261 0.213	0.192 0.216	0.020 -0.007	0.241 0.182	-0.094 -0.122	0.142 0.075	0.725 0.613	-0.005 -0.034
Time of head emergence		-	0.271 0.242	-0.016 -0.048	0.307 0.135	0.084 0.069	0.220 0.117	-0.077 -0.024	0.283 0.252	-0.247 -0.344	-0.693 -0.479
Tiller angle			-	-0.281 -0.208	-0.131 -0.047	0.006 0.045	0.184 0.106	0.039 0.032	-0.082 -0.030	-0.185 -0.173	-0.590 -0.172
Tiller length				-	0.397 0.354	0.245 0.172	0.220 0.226	0.310 0.219	0.672 0.647	0.578 0.428	-0.542 -0.302
Leaf number					-	0.131 0.078	-0.081 0.038	0.211 0.144	0.515 0.451	0.255 0.230	-[3] -0.170
Leaf width						-	0.401 0.307	0.605 0.443	0.610 0.467	0.389 0.227	-0.234 -0.127
Leaf length							-	0.368 0.294	0.534 0.454	0.436 0.330	-0.163 -0.107
Stem diameter								-	0.701 0.462	0.273 0.122	0.124 0.051
Tiller weight									-	0.607 0.399	-0.645 -0.297
Fresh weight of the plant										-	-0.059 0.019
D_{vitro}											-

1 First line : genotypic correlation coefficient; second line: phenotypic correlation coefficient.
2 Based on 50 plants.
3 Genotypic variance was negative.

king feature of this table is the strong negative, genotypic correlation between time of head emergence and D_{vitro}. The simple correlation coefficient between these 2 characteristics for the 121 plants was $r = -0.427$ ($P < 0.01$ with 119 degrees of freedom). These correlations meant that tillers of the same maturity, sampled from early-heading plants, had a higher digestibility than those from late-heading plants.

D_{vitro} was linearily related to time of head emergence, calculated between the 121 means of the two characteristics ($P < 0.05$) (Fig. 1). From this figure the large variation in D_{vitro} occurring in a maturity group is evident. A delay of one week in head emergence meant a drop in D_{vitro} of 0.77% digestibility units, averaged over three harvests.

Other characteristics showing a strong genotypic correlation with D_{vitro} (Table 8) were tiller angle, tiller length and tiller weight. When considering these relationships, the strong one between D_{vitro} and time of head emergence has to be taken into account. The absence of a strong correlation between tiller length and time of head emergence, for example pointed to the direct effect of tiller length on D_{vitro}: short tillers had a higher digestibility than longer tillers, while the stronger, positive correlations between time of head emergence with tiller angle and tiller weight suggested an indirect effect of these 2 characteristics on D_{vitro}.

The genotypic correlation between tiller angle and D_{vitro} was high and negative. As tiller angle was a measure of the erectness of the plant (the lower the value, the more erect the plant), the relationship between these two characteristics implied that tillers collected from erect-growing early-heading plants (the genotypic correlation coefficient between the latter 2 characteristics was 0.271) had a higher digestibility than those from prostrate plants.

That a high leaf number did not necessarily mean high digestibility is evident (Table 8) from the negative phenotypic correlation between leaf number and D_{vitro} (the simple correlation coefficient between them for the 121 plants was $r = -0.265$, $P < 0.01$ with 119 degrees of freedom), because plants having many leaves on 15 tillers belonged to the late-heading plants characterized by a low D_{vitro}. Moreover, it was found in the second harvest of 1975 that tillers of late-heading plants tended to have more dead leaves than tillers from early plants ($r = 0.313$, $P < 0.01$ for 119 degrees of freedom) (data not presented). However, no significant relationship between D_{vitro} and number of dead leaves was established.

The repeatabilities of the measured characteristics, the means per harvest and the heritabilities in the wide sense on an individual plant basis are presented in Table 9. As the repeatability and the heritability were not estimated from the same analysis of variance, repeatability did not set the upper level of heritability - heritability exceeded repeatability for most characteristics. Tiller number, leaf width, leaf length and tiller weight displayed high repeatability, while the repeatability of tiller angle, fresh weight and tiller length were low. The last-named was in fact negative, for which the poor 1974 harvest must be held responsible. Tiller weight was less affected by harvests than tiller length, though a strong phenotypic and genotypic correlation (Table 8) existed between the two characteristics. However, in the 1974 harvest there was a higher dry-matter percentage compared with the other two harvests (data not presented), which

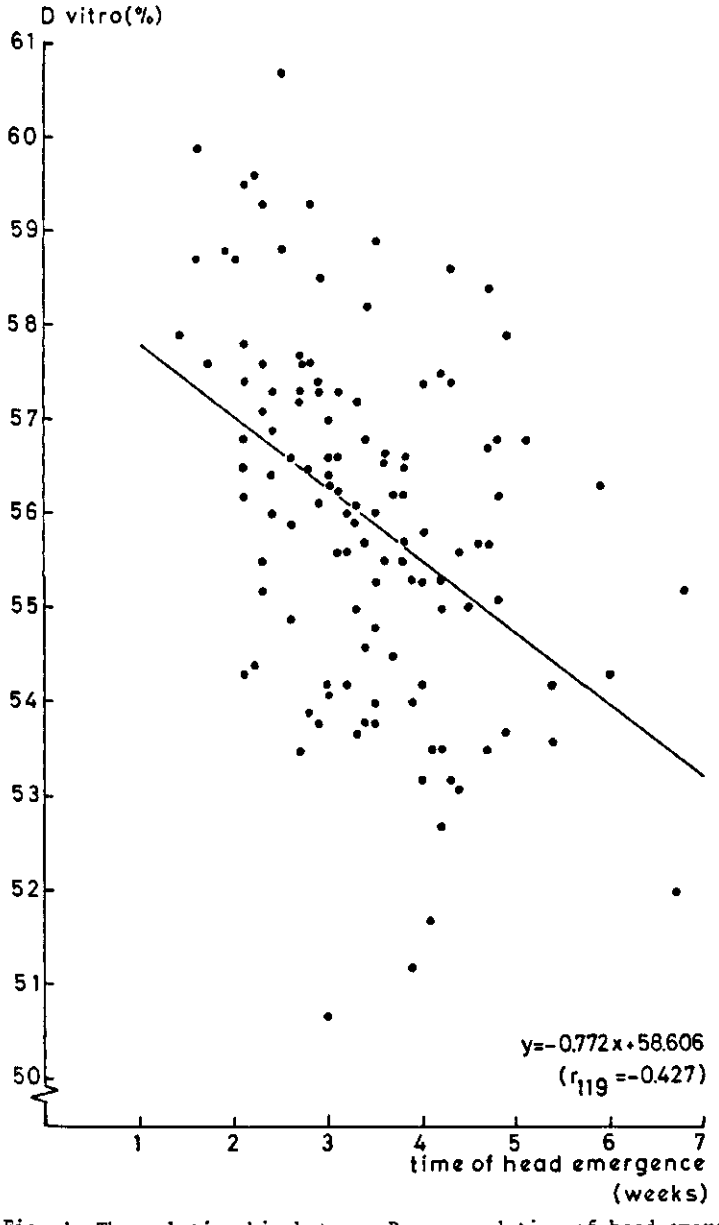

Fig. 1. The relationship between D_{vitro} and time of head emergence.

compensated for the lower fresh weight of the harvest in 1974 due to the shorter tiller length. For that reason the three tiller weight means were almost similar. Fresh weight of the plant consequently evinced a low repeatability, which is also evident from the three different means. The heritabilities were invariably high, tiller angle and stem diameter having the lowest values. Low repeatability did not necessarily mean low heritability, as is clear from the tiller length. But when both values are small this is an

Table 9. Repeatabilities, means per harvest and heritabilities in the wide sense on an individual-plant basis.

Character	Repeatability	Mean per harvest			Heritability in the wide sense
		1974	1975a	1975b	
Tiller number	0.62	357	397	450	0.56
Time of head emergence (week)	0.21	4	2	4	0.64
Tiller angle	0.13	1.75	1.83	1.54	0.41
Tiller length	-0.12	42	66	64	0.70
Leaf number (15 tillers)	0.30	85	77	85	0.51
Leaf width (mm)	0.64	9	10	9	0.67
Leaf length (cm)	0.53	22	23	22	0.67
Stem diameter (mm)	0.43		3.4	3.3	0.45
Tiller weight (g) (15 tillers)	0.54	20	19	20	0.70
Fresh weight of the plant (kg)	0.16	1.0	2.2	1.6	0.52
D_{vitro} (%)[1]	0.19	55.0	57.3	57.0	0.75

1. Based on 50 plants.

indication of the low reproducibility of that characteristic, tiller angle being one such characteristic.

The results of the multiple regression analysis, with D_{vitro} as dependent variable, are shown in Table 10. The scatter diagram of the residuals versus the fitted y-values revealed an even distribution around the zero line of the means of the 121 plants, indicating that no data transformation was required. The standard error estimated from close neighbours agreed with the standard deviation from the full equation, which showed that there was no lack of fit. Time of head emergence exerted the greatest influence upon D_{vitro}, followed by tiller length and stem diameter. Time of head emergence, leaf width, stem diameter and tiller weight were finally selected as the best predictors of D_{vitro} at $p = C_p = 5$. A smaller number of variables than the ones present in this equation caused great model bias. The full equation explained 32.5% of the variation observed in D_{vitro}, while the selected subset equation accounted for 28.8%.

The regression analysis measured only the mutual association between the dependent and the independent variables without regard to the cause. Path coefficients can elucidate the relationships between the dependent and independent variables by separating the direct effects of each independent variable from the indirect effects on the dependent variable via other independent variables. The results of the pathway analysis for D_{vitro} and the characteristics of the finally selected subset equation of Table 10 are shown in Table 11.

Though the strongest simple correlation was that between D_{vitro} and time of head emergence, the pathway analysis showed that the direct effect of tiller weight was greater than the time-of-head-emergence effect, due to the indirect, positive influence of stem diameter via tiller weight. The absence of a significant simple correlation between D_{vitro} and stem diameter, which showed a high direct effect on D_{vitro} (0.266), was due

Table 10. Multiple regression with D_{vitro} as dependent variable of 121 plants.

Variable	Partial regression coefficient	t-value	Relative influence
Full equation			
Tiller number	-0.001	0.6	0.08
Time of head emergence	-0.540	2.7	0.29
Tiller angle	-0.172	1.4	0.12
Tiller length	-0.074	2.0	0.24
Leaf number	0.011	0.4	0.04
Leaf width	-0.379	1.6	0.16
Leaf length	0.014	0.2	0.02
Stem diameter	1.993	2.1	0.24
Tiller weight	-0.096	0.9	0.18
Fresh weight of the plant	0.007	0.9	0.17
Constant	64.582		
$F^{10}_{110} = 5.3^{**}$			
Residual mean square = 2.678			
Squared multiple correlation coefficient = 0.325			
Subset equation			
Time of head emergence	-0.585	3.9	0.32
Leaf width	-0.237	1.0	0.10
Stem diameter	2.226	2.6	0.27
Tiller weight	-0.182	3.4	0.34
Constant	56.424		
$F^{4}_{116} = 11.7^{**}$			
Residual mean square = 2.678			
Squared multiple correlation coefficient = 0.288			

** $P < 0.01$

to the indirect path value of stem diameter via tiller weight (-0.219). Time of head emergence did not act through one of the other characteristics. The direct effect of leaf width (-0.102) was small, though its simple correlation with D_{vitro} was significant. Its direct effect was masked by the high indirect effects of leaf width via tiller weight (-0.210) and stem diameter (0.141).

By multiplying tiller number, tiller weight and D_{vitro}, an estimation of Y_{DOM} at IHE could be obtained, which was related to the remaining plant characteristics (Table 12). Tiller length, leaf number, leaf length and fresh weight of the plant especially, showed

Table 11. Path coefficients for D_{vitro} and 4 plant characteristics of 121 plants. r = simple correlation coefficient.

D_{vitro} vs time of head emergence	
Direct effect	-0.320
Indirect effect via leaf width	-0.009
Indirect effect via stem diameter	-0.003
Indirect effect via tiller weight	-0.095
	r = -0.427
D_{vitro} vs leaf width	
Direct effect	-0.102
Indirect effect via time of head emergence	-0.030
Indirect effect via stem diameter	0.141
Indirect effect via tiller weight	-0.210
	r = -0.201
D_{vitro} vs stem diameter	
Direct effect	0.266
Indirect effect via time of head emergence	0.004
Indirect effect via leaf width	-0.054
Indirect effect via tiller weight	-0.219
	r = -0.003
D_{vitro} vs tiller weight	
Direct effect	-0.372
Indirect effect via time of head emergence	-0.081
Indirect effect via leaf width	-0.057
Indirect effect via stem diameter	0.156
	r = -0.354
Unexplained	0.844

strong correlations with Y_{DOM}. The last-named correlation thus showed the high predictive value of the fresh weight of the plant taken about 7 weeks after IHE on Y_{DOM} at IHE. Yield determinations on fresh material are subject to sampling errors due to a varying dry-matter content during the day. In an earlier study with the 121 plants, however, the

Table 12. Simple correlation coefficients between the estimated Y_{DOM} at IHE and various plant characteristics of 121 plants.

Characteristic	
Time of head emergence	-0.065
Tiller angle	-0.189*
Tiller length	0.492**
Leaf number	0.443**
Leaf width	0.254**
Leaf length	0.421**
Stem diameter	0.189*
Fresh weight of the plant	0.853**

* $P < 0.05$

** $P < 0.01$

simple correlation coefficient between the fresh weight of the plant at seed harvest and the dry weight of the plant at that time was 0.949 with 119 degrees of freedom (data not presented). In view of this high correlation and the ease with which the characteristic could be recorded, possible inaccuracies, if present, were incorporated in the determination.

2.2.3 Discussion

The variation observed in D_{vitro} of tillers of the same maturity could be largely explained by their difference in age, as expressed by the time-of-head-emergence characteristic (Tables 8, 10 and 11), which accounted for 18.2% of the variation, while the remaining nine characteristics explained 14.3%.

Ageing of the grass plant causes morphological and chemical changes within the plant, affecting digestibility. From a vegetative stage, at which the tillers consist only of leaf sheaths that surround young, unexpanded leaf tissue, tillers change in the process of ageing into a reproductive stage through stem elongation, causing a decrease in the proportion of cell contents and an increase in the proportion of cell-wall constituents, these consisting of cellulose, hemicellulose and lignin.

Early- and late-heading plants show different growth rates and ageing will therefore affect both types differently. Early-heading plants will reach a defined morphological stage earlier than late-heading plants because of their faster growth rate. Consequently, material of similar morphological development in early- and late-heading plants will be different in age. In the present study the average time span between the first and last tillers sampled (i.e. tillers with the tip of the inflorescence just visible when the plant had developed 10 or more flowering heads) was seven weeks (Table 7).

The processes described above take place in both temperate and tropical grasses, but ageing in tropical grasses is more intense because they continuously show internode elongation in the vegetative and generative stages. In temperate grasses, internodes hardly elongate at all during the vegetative stage. Late-heading tropical grasses extend stem elongation over a much longer period than early-heading plants do. Though the growing point in late-heading plants remains vegetative relatively longer than in early-heading plants, stem elongation in late-heading plants is known to go long before inflorescence development, thus resulting in a stronger ageing effect on the part of late-heading plants than of early plants compared at the same maturity. This leads to an increased proportion of cell-wall constituents, especially the lignin content, which adversely affects digestibility. Moreover, tissue of slow-growing plants, i.e. late-heading plants, is more lignified than that of fast-growing plants, i.e. of early-heading plants (Sullivan, 1969).

Besides differences in age between plants, as stated above, differences in age of leaves occur within plants as well: higher inserted leaves are younger than leaves inserted at the base of the grass tiller. Wilson (1976) investigated the relationship between the level of insertion of leaves on a tiller and quality in *Panicum maximum* Jacq. var. *trichoglume* Eyles (green panic) at a common development of the leaf (full expansion of the leaf blade) and in a constant environment. The percentage of cell-wall contents of

both leaf blade and leaf sheath increased with higher level of insertion (i.e. leaves formed later) compared when the leaf blade was just fully expanded. Therefore leaf blades and sheaths of lower insertion level (i.e. formed earlier) were higher in in vitro digestibility than those inserted higher on the tiller. But ageing (compared over a time span of 20 days after full expansion) altered the expression of these characteristics. Leaf blades and sheaths of lower insertion levels had a more rapid percentage increase in the cell-wall constituents than those of higher insertion levels. The proportion of cell-wall constituents of the high-inserted blades and sheaths was, however, still higher than those of lower insertion. The differences in cell-wall constituents between the different levels of insertion were no longer as great as when measured at full expansion. Regarding in vitro digestibility of leaf blades, the situation was reversed after 20 days: leaf blades of higher insertion level now had a higher digestibility than those of lower insertion. This effect was explained by the faster senescence of the leaves formed earlier. The digestibility of the leaf sheaths did not show a consistent change with insertion level during ageing.

A grass tiller produces leaves up to head emergence and thus late-heading plants have more time to produce leaves than early-heading plants. Moreover, late-heading plants produce more leaves than early-heading plants, as is evident from the positive genotypic correlation between time of head emergence and leaf number (Table 8). The first formed leaves of late-heading plants are exposed to ageing for longer than those of early-heading plants. This, and the greater number of leaves ageing affect digestibility more adversely than the earlier formed leaves at lower insertion levels of early plants.

Walters et al. (1967) held the higher amount of dead material accumulated by late varieties responsible for the lower digestibility of late varieties compared at a similar growth stage with early varieties. In setaria there was a significant, positive correlation between time of head emergence and number of leaves, but no significant correlation was found between D_{vitro} and number of dead leaves. It has to be realised, however, that the dead leaves were first-formed leaves. These leaves are smaller in size than those developed later as found by Wilson (1976) in green panic and they therefore contribute relatively little to the total tiller.

Although environmental influences on D_{vitro} during the 7-week sampling period cannot be altogether excluded, changes in climatic conditions cannot explain the differences observed in D_{vitro} of early- and late-heading plants. Mean daily temperatures were virtually constant throughout the growing season in Kitale, while no water deficit occurred during the period of observation.

In addition to their being derived from early-heading, erect-growing plants, tillers of high digestibility were characterized by short length, narrow leaves and light weight (Table 8). Some of these relationships agree with those found by other authors. Ross et al. (1970) reported a significant negative correlation between plant height and digestibility in *Bromus inermis* Leyss. (smooth bromegrass). High digestibility in *Phalaris tuberosa* L. (bulb canary-grass) was associated with short tillers (Clements, 1973). Sleper & Drolsom (1974) found a significant, negative correlation between plant height and digestibility in smooth bromegrass, while Ross et al. (1975) reported a significant correlation between stem weight and digestibility in *Andropogon gerardi* Vitman (big bluestem

grass). Burton et al. (1969) introduced a dwarf gene into *Pennisetum typhoides* (Burm.) Stapf and C.E. Hubb. (pearl millet), that consequently shortened the internode length and improved stem quality.

Tiller length did not appear in the finally selected subset equation, but in view of the high genotypic correlation between this characteristic and tiller weight (Table 8) and the fact that tiller weight exerted the largest direct influence on D_{vitro} (Table 11), it can be concluded that tiller length in setaria is a characteristic which plays an important part in determining digestibility.

The genotypic correlation between stem diameter and D_{vitro} was positive, but small (Table 8). The direct influence of stem diameter on D_{vitro} was relatively large and positive, but was masked by the negative, indirect effect via tiller weight (Table 11). The cocksfoot plants selected for high digestibility possessed wider stems than the plants selected for low digestibility (Breese & Davies, 1970).

Clements (1973) reported a significant negative correlation between digestibility and stem diameter in bulb canary-grass, while a positive correlation between these characteristics was found in smooth bromegrass by Sleper & Drolsom (1974). In *Hemarthria altissima* (Poir.) Stapf and Hubbard (limpo grass) a tetraploid introduction was reported, that was characterized by fewer leaves, thicker stems and a higher digestibility at 5 weeks than diploid introductions (Schank et al., 1973). Although the difference in quality might have been caused by the diploid and tetraploid nature of the material under study, the observed differences in quality could be traced back to anatomical differences. The tetraploid introduction had a smaller vascular-bundle area and showed hardly any increase in the percentage of lignin and no decrease in digestibility with age compared to the diploid introductions. Lignification therefore seemed to be more pronounced in plants with a larger vascular-bundle area. It should be emphasized that the tetraploid introduction occurred naturally and was not artificially derived from a diploid.

In setaria no clear picture as to the influence of stem diameter in D_{vitro} emerges and its role is only understood when the strong interrelationship between stem diameter, tiller weight and tiller length are taken into account as well.

In view of the significant differences between the 121 plants and the high heritabilities shown (Table 9), there is ample scope for selection of each of the measured characteristics in the source population of 4000 Nandi I plants, of which the 121 plants represented a random sample. It should be realized that the heritabilities were obtained from one location and that a possible genotype × location interaction, which would lower the estimated heritability values, could not be estimated. The influence of the different harvests on the reproducibility of the measured characteristics was expressed in the repeatability (Table 9). The repeatability values varied to a greater extent than the heritabilities. Tiller length even indicated a negative estimate of the repeatability, while its heritability was one of the highest. The heritability was estimated from the clonal components of variation due to environmental and genetic effects, while the repeatability was obtained from the variation due to environmental effects (i.e. harvest to harvest differences). For tiller length these differences were in fact large and resulted in a negative estimate, while the environmental differences within clones due to replicate effects were not as large, and led to a high heritability estimate. Tiller angle,

fresh weight and D_{vitro} also showed low repeatability and those characteristics are thus sensitive to year-to-year differences. Tiller angle moreover showed a lower heritability than the other characteristics and is therefore very dependent on environmental effects.

Selection of early-heading plants with fine tillers will improve digestibility. The repeatability and the heritability of tiller weight, the characteristic which has a great influence on D_{vitro} in the subset equation (Tables 10 and 11) were high, hence the response to selection for this characteristic will be great. A negative response in dry-matter yield by selecting these fine-textured, short plants is, however, expected. In fact, Burton et al. (1969) found that by introducing a dwarf gene into pearl millet, dry-matter yield was significantly reduced, while in vitro digestibility was increased. In setaria the loss of dry-matter yield could be compensated by selecting plants with a high tiller number. Among 13 high-digestible plants (the mean D_{vitro} was 59.3%, averaged over 3 harvest) out of the 121 plants three had 25% more tillers per unit area than the other 10, as calculated from the number of tillers and the basal circumference; these values were 35 and 28 tillers per dm^2, respectivily.

According to Stobbs (1973a) sward bulk density, calculated as the dry-matter yield of the grass divided by its average height, was the major factor affecting the size of bite taken by cows grazing three tropical grass species. Stem content and leaf/height ratio are incorporated in the sward bulk density. Large bite prehension is likely to be more difficult on tropical pasture swards than on temperate grass swards because of the low bulk density and the higher stem content of tropical grasses (Stobbs, 1973b). Dirven (1977) suggested that the low bulk density of tropical grasses is caused by low tiller density and continuous stem elongation. Thus by selecting plants with many tillers to compensate the loss of dry-matter yield caused by digestibility improvement through selection, herbage intake will be simultaneously increased. A high tiller density might adversely affect the seed-producing ability. The bulk density of the 121 setaria plants was calculated as the contents of the plant from the plant heigth at IHE, the circumference at the base of the plant and the circumference at the height of the flag leaf (data not presented). The genotypic correlation between the bulk density and the fresh weight of the plant at seed harvest amounted to 0.871. Bulk density and fresh weight showed a genotypic correlation with tiller number, of 0.536 and 0.725, respectively. From these correlations it is evident that the fresh weight of the plant at seed harvest possessed a high predictive value of the bulk density of the plant at IHE and showed a better correlation with tiller number than with bulk density. This is corroborated by the strong simple correlation coefficient between fresh weight and Y_{DOM} at IHE (Table 12).

The absence of a correlation between time of head emergence and estimated Y_{DOM} (Table 12) showed that it is possible to select plants with a high Y_{DOM} in all heading groups. The lower digestibility of the late-heading plants was made up for by the higher tiller weight, while in the early plants the loss in tiller weight due to the finer tiller texture, was compensated by their higher digestibility and tiller number, which resulted in an equal Y_{DOM} for both heading groups.

2.3 INTRA-VARIETAL COMPARISONS MADE AT THE SAME TIME ON THE WHOLE PLANT

2.3.1 Material and methods

In 1976 the 121 plants described in Section 2.2.1 were compared at different times of regrowth, which was confounded with the replicates.

On 12 April 1976 the three replicates were top-dressed with 100 kg of nitrogen per hectare after a cleaning cut. Due to a severe drought the whole trial was cut back on 11 May and top-dressed with 50 kg of nitrogen. Each plant of Replicate 1 was cut after three weeks of regrowth. The same was done for the plants of Replicate 3 after 6 weeks of regrowth, while Replicate 2 was cut 9 weeks after the cleaning cut.

The fresh weight of each plant was determined. A sample of 500 g of fresh material (or less if the total weight of the plant was less than 500 g) was dried, weighed, ground and analysed for D_{vitro}. Another sample of 250 g of fresh material (or less if not enough material was available) was seperated into leaves, stems and dead material. The fractions were dried and weighed.

Y_{DOM} of each plant was related per regrowth period to the plant characteristics as measured in Section 2.2 (means of three harvests per replicate) through a multiple regression analysis.

The whole series of measurements was repeated after the final cut (after 9 weeks' regrowth) of Replicate 2 on 12 July 1976. Replicates 1 and 3 were then cut back and the three replicates were top-dressed with 100 kg of nitrogen per hectare. A comparable pattern of harvesting was followed with times of regrowth of 4 (Replicate 1), 8 (Replicate 3) and 12 weeks (Replicate 2). The yields of this second series will not be discussed here, but will be added per replicate to those of the first series for the determination of the total yield in Section 6.3.1.

As replicates were confounded with time of regrowth, the error component in the analysis of variance would contain the regrowth effect. Therefore the value of each plant was expressed relative to the mean of the replicate in which it occurred, after which an analysis of variance according to Harvey (1976) was carried out corrected for blocks to determine the heritability in the wide sense (Table 5).

2.3.2 Results

The ranges in Y_{DM}, D_{vitro}, Y_{DOM} and % leaf of the 121 plants with their respective means and coefficients of variation are presented in Table 13. Dry-matter yield increased by 394% during 6 weeks of growth, while the increase amounted to 294% for Y_{DOM}. The coefficient of variation for Y_{DM} and Y_{DOM} within the 121 plants did not differ markedly over the various regrowth periods. Digestibility dropped by 12.6% units after 3 to 9 weeks' regrowth, which is 0.3% units per day. The coefficient of variation for D_{vitro} was much smaller than that for Y_{DM} and Y_{DOM} and increased with the ageing of the plant.

The coefficient of variation for leaf percentage increased with longer regrowth periods: the coefficient of variation after 3 weeks' of regrowth was smaller than after 9 weeks. The percentage of dead material accumulated was 0, 3.0 and 3.9% for 3, 6 and 9

Table 13. Ranges, means and coefficients of variation (% CV) of Y_{DM}, D_{vitro}, Y_{DOM} and % leaf at 3 periods of regrowth.

Period of regrowth	Y_{DM} (g/plant)			D_{vitro} (%)		
	range	mean	% CV	range	mean	% CV
3 weeks	4-166	79	43.9	58.0-67.7	63.7	2.7
6 weeks	2-465	224	46.7	49.1-62.2	56.8	4.8
9 weeks	81-820	390	36.2	41.5-61.1	51.1	6.2
Period of regrowth	Y_{DOM} (g/plant)			% leaf		
	range	mean	% CV	range	mean	% CV
3 weeks	3-101	50	43.5	32.2-87.5	60.0	15.7
6 weeks	1-265	126	45.5	19.6-80.0	39.6	24.1
9 weeks	43-408	197	34.7	13.8-50.0	24.3	24.9

weeks' regrowth, respectively. Differences between plants for the relative values of Y_{DM}, D_{vitro} and Y_{DOM} were significant ($P < 0.01$). Heritabilities in the wide sense on an individual plant basis of Y_{DM}, D_{vitro} and Y_{DOM} were 0.31, 0.25 and 0.50, respectively.

The simple correlation coefficients between Y_{DM}, D_{vitro} and Y_{DOM} and % leaf are shown in Table 14. Apart from the dry-matter yield after 3 weeks of regrowth, Y_{DM} showed a significant, negative correlation with D_{vitro} ($P < 0.01$). For 3 weeks' regrowth this relationship was linear at $P < 0.10$, while for 6 and 9 weeks Y_{DM} and D_{vitro} were linearly related at $P < 0.01$. In Figure 2 the regression of Y_{DM} on D_{vitro} is borne out for the 6 weeks' regrowth period as an example of the wide variation that occurred in both D_{vitro} and Y_{DM}. The three regression lines between those two characteristics for the 3, 6 and 9 weeks' regrowth periods are presented in Figure 3. The lines were almost parallel, indicating that D_{vitro} dropped at the same rate for plants of different age with increasing Y_{DM}. A higher leaf percentage had a significant, positive effect on D_{vitro}, while Y_{DM}, Y_{DOM} and leaf percentage displayed a significant, negative relationship at 3 and 6 weeks' regrowth (Table 14). The absence of a significant relationship between yield and leaf percentage after 9 weeks was due to the large amount of stem.

Table 14. Simple correlation coefficients between Y_{DM}, D_{vitro}, Y_{DOM} and % leaf.

Correlation	Period of regrowth		
	3 weeks	6 weeks	9 weeks
Y_{DM}-D_{vitro}	-0.174	-0.396**	-0.385**
D_{vitro}-% leaf	+0.238**	+0.183*	+0.238**
Y_{DM}-% leaf	-0.352**	-0.289**	-0.066
Y_{DOM}-% leaf	-0.342**	-0.283**	-0.029

* $P < 0.05$
** $P < 0.01$

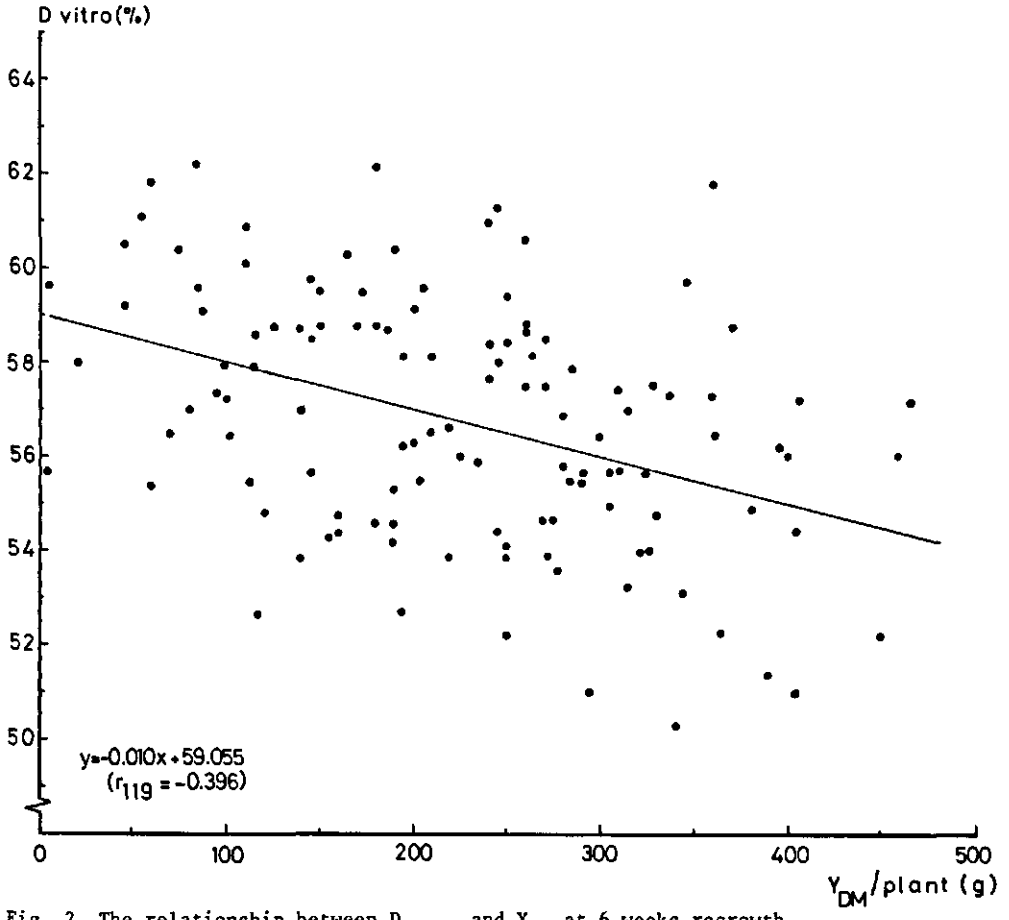

Fig. 2. The relationship between D_{vitro} and Y_{DM} at 6 weeks regrowth.

Y_{DOM} was related to the characteristics measured in the 1974 and 1975 crops (Section 2.2.1), that is Y_{DOM} of each regrowth period as the dependent variable and the means of the three harvests of the respective replicate as the independent variables (Table 15). The various plant characteristics (the independent variables) were measured at the same morphological stage (except for tiller number), while the yield data refer to observations made on the same date. Tiller number and, logically, fresh weight of the plant at time of seed harvest showed the highest correlation with Y_{DOM}. After 3 weeks' regrowth these two characteristics exerted the greatest influence on Y_{DOM}, while after 6 weeks and 9 weeks' tiller weight was equally important, or more so.

After 6 and 9 weeks' regrowth the contribution of the leaf fraction to Y_{DM} and Y_{DOM} was only 39.6 and 24.3% (Table 13), while the remainder of the yield was made up of stems and dead material. Tiller weight could therefore have a large influence on both yield characteristics. Early-heading plants had a significantly higher yield level at 3 weeks of regrowth, but this relationship was not significant at 6 and 9 weeks. The determined characteristics accounted for more than 50% of the variation observed in Y_{DOM} and their

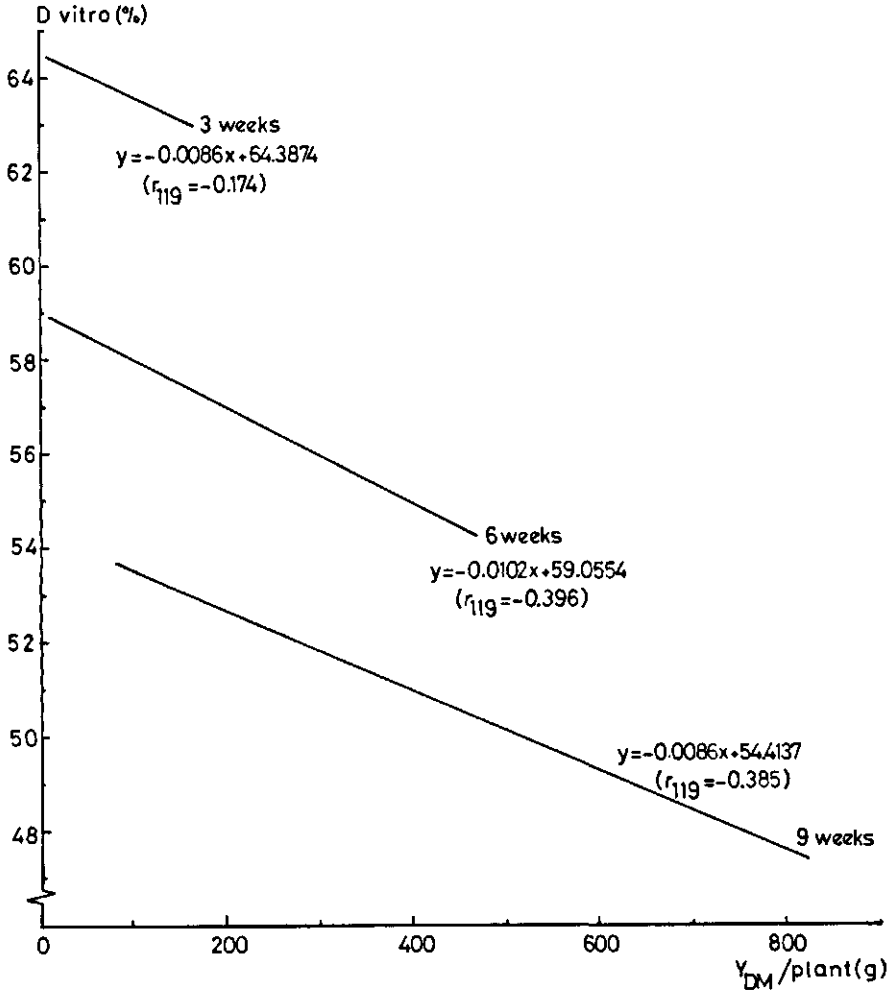

Fig. 3. The relationship between D_{vitro} and Y_{DM} at 3 periods of regrowth.

joint contribution was highly significant.

From Figure 2 the wide variation for Y_{DM} and D_{vitro} is evident. It seems possible therefore to select plants that combine both high digestibility and high Y_{DM} by setting culling levels for both characteristics, notwithstanding their negative correlation. After 3 weeks' regrowth, 20 plants were selected with Y_{DM} higher than 100 g per plant and D_{vitro} higher than 63.0%. The selected plants showed an increase of 33%, 11% and 35% in number of tillers, tiller weight and fresh weight of the plant, respectively, compared to the population of 121 plants, while the expression for the remaining characteristics, including % leaf, remained virtually the same. After 6 weeks' regrowth, 17 plants were selected with Y_{DM} higher than 250 g per plant and D_{vitro} exceeding 57% - the same number of plants was selected after 9 weeks' regrowth with levels for Y_{DM} and D_{vitro} set at 420 g and 51%, respectively. For the last two regrowth periods, tiller number and fresh weight increased by approximately 15%, while the other characteristics displayed only

Table 15. The relationship between Y_{DOM} at different regrowth periods and various plant characteristics. r = simple correlation coefficient; rel. inf. = relative influence.

Characteristic	3 weeks		6 weeks		9 weeks	
	r	rel. inf.	r	rel. inf.	r	rel. inf.
Tiller number	0.628**	0.32	0.541**	0.36	0.508**	0.22
Time of head emergence	-0.242**	0.04	-0.144	0.13	-0.132	0.05
Tiller angle	0.036	0.15	-0.028	0.06	-0.209*	0.08
Tiller length	0.465**	0.09	0.355**	0.11	0.452**	0.04
Leaf number	0.297**	0.08	0.335**	0.05	0.191*	0.02
Leaf width	0.197*	0.02	0.231*	0.04	0.211*	0.06
Leaf length	0.401**	0.06	0.378**	0.07	0.374**	0.12
Stem diameter	0.172	0.01	0.175	0.01	0.098	0.18
Tiller weight	0.429**	0.17	0.477**	0.50	0.482**	0.28
Fresh weight	0.745**	0.39	0.632**	0.26	0.641**	0.28
F_{110}^{10}	22.2 **		13.2 **		13.6 **	
Squared multiple correlation coefficient	0.668		0.545		0.554	

* $P < 0.05$
** $P < 0.01$

marginal changes. Thirteen plants occurred in two out of the three selected groups of plants.

2.3.3 Discussion

The final criterion for assessing a plant on nutritive value is its yield of digestible organic matter, this being the product of quality and quantity. There is little sense in improving quality at the expense of dry-matter yield, if indiscriminately increasing yield were to cause a correlated negative response in quality, resulting in a decreased intake by the grazing animal.

In view of the results dealt within Section 2.2 (Table 12) the expectation was expressed that digestibility could be improved, when compared at the same growth stage, without loss in dry-matter yield by selecting early, dense-tillering plants with a fine texture.

This expectation was based on the assumption that loss in one characteristic (tiller weight) could be compensated by gain in another (tiller number). The total Y_{DOM} would therefore remain unchanged compared with the population mean.

The results presented in this chapter suggest that, due to the negative relationship between D_{vitro} and Y_{DM} (Table 14 and Fig. 3), simultaneous improvement of both characteristics is hard to attain. Negative relationships between forage yield and digestibility were also reported by Carlson et al. (1969) in *Phalaris arundinacea* L. (reed canary-grass), by Clements (1970) in bulb canary-grass, by Coulman & Knowles (1974) in *Agropyron*

cristatum L. (crested wheatgrass) (not significant) and by Ross et al. (1975) in big bluestem grass.

Raymond (1969) postulated "If one genotype is of higher yield than another when both have the same level of digestibility, the first genotype is likely to be of higher digestibility when both are harvested at the same yield". Implication of this assertion in practical breeding will result in the selection of fast-growing plants, which reach a certain yield level earlier than slower-growing plants and, as is evident from Section 2.2, have a higher digestibility in consequence. Selection for dry-matter yield on a time basis will therefore have a correlated positive response in digestibility, but only when the selected plants are compared with the original population at the same morphological stage.

The selection of fast-growing plants will also affect the total annual dry-matter production as varieties based on these plants will allow more grazings or cuts per year due to their vigorous regrowth. From Table 8 the positive, genotypic correlation between time of head emergence and tiller angle is evident, indicating that fast-growing plants (i.e. early-heading plants) are more erect than slow-growing plants (i.e. late-heading plants), which could adversely affect the persistence of these fast-growing plants.

The heritabilities in the wide sense of Y_{DM} and Y_{DOM} were great and indicated that mass selection for yield was feasible. The heritability of Y_{DOM} was greater than that of Y_{DM} because the product of D_{vitro} and Y_{DM} showed greater genetic variation than Y_{DM}.

In a comparable study on Rhodes grass Boonman (1978b) found heritabilities in the wide sense for Y_{DM} and Y_{DOM} to be 0.15. These data, however, refer to a narrowed population in which the amount of genetic variation had been reduced by selection.

The wide variation for D_{vitro} and Y_{DM} (Fig. 2) permitted the selection of a group of plants at each regrowth period with above-average values for these two characteristics. However, D_{vitro} was only relatively improved by 1-3% while Y_{DM} was raised by 32-51%. The ultimate increase of Y_{DOM} was therefore largely caused by increased dry-matter production rather than by improved digestibility. Marked correlated responses, too, were only obtained from production characteristics (tiller number and fresh weight of the plant), while the other characteristics showed minor changes. In view of the variation of Y_{DM} and D_{vitro} in the population of 121 plants (Table 13) it would therefore appear to be more rewarding to select for dry-matter yield than to obtain marginal increases in digestibility. The consequence of selection in this direction is that a slight shift towards earliness of heading is inevitable.

The variability and the range for D_{vitro} increased with the length of the regrowth period (Table 13). This contrasted with the results obtained by Hacker & Minson (1972) who reported a larger range in values of in vitro digestibility at 4 weeks' regrowth than after 8 or 12 weeks of regrowth of various setaria species. The three *Setaria anceps* Stapf ex Massey introductions in their study, however, only showed a slight increase in the range of digestibility. It should be emphasized that those data refer to observations made throughout the year. In summer time, from December to April, older regrowth had a greater range in digestibility than younger regrowth, while during the winter, from June to September, the opposite occurred. Hacker & Minson (1972) concluded that selection should be based on data obtained from the older material in summer. Milford &

Minson (1968), Minson (1971a) and Minson (1972) found, too, that the range in digestibility values of varieties of Rhodes grass, of *Panicum* species and of six different grasses, respectively, was greater in regrowth older than 1 month than in monthly regrowth. Minson (1972) concluded that screening for digestibility should be done at mature stages of growth-differences in digestibility were most likely to occur then. This suggestion was supported by the fact that only slight differences between species and varieties were detected at monthly regrowth, which prompted Milford & Minson (1968) to conclude that the prospects for selecting a variety of Rhodes grass with superior feeding value were not good.

Under farming conditions regrowth periods as long as those applied in the experiments described above are not the practice. Therefore, if selection is to be based on regrowth of high age, a strong correlation between young and old regrowth for digestibility is anticipated. Simple correlation coefficients between the three regrowth periods used in this study for D_{vitro} were significant ($P < 0.05$) for 3 and 6 weeks, not significant for 3 and 9 weeks and significant ($P < 0.01$) for 6 and 9 weeks. Correlations for Y_{DM} and for Y_{DOM} between any two of the three regrowth periods, on the other hand, were all significant at the $P = 0.01$ level. D_{vitro} therefore appeared to be less reliably reproduced at different stages of regrowth than the two yield characteristics. As no specific recommendation emerged from these results as to the age at which selection for D_{vitro} should be applied, it is concluded that selection should be carried out at the growth stage suitable for grazing, which is approximately after 4-6 weeks of regrowth following onset of the rains.

Rhodes (1973a) considered tiller angle and leaf length as the most important factors determining canopy structure, tiller angle determining the angle of presentation of the photosynthetic material to the incoming light and leaf length controlling the height of the canopy. These two characteristics were closely related to the dry-matter yield in the first cut of swards made up out of the F_1 generation families of a diallel between six perennial ryegrass and Italian ryegrass varieties and populations (Rhodes, 1973b). Groups of genotypes with an extreme expression of the various canopy characteristics were selected within the six highest-yielding families of the diallel (Rhodes, 1975) and were studied for sward yield at approximately 35-day intervals. Selection for the long-leafed habit increased dry-matter yield in the first year in general. No regular increase in yield of the high tiller-angle selections were obtained, while a lack of persistence was observed for these selections. In the setaria population of the 121 plants the correlation between Y_{DOM} and tiller angle was only significant at 9 weeks (Table 15), while leaf length displayed a significant positive correlation with Y_{DOM} at the 3 periods of regrowth. Both characteristics, however, exerted a slight relative influence in the multiple regression (Table 15). Tiller number and Y_{DOM} showed a significant positive correlation, so that tiller number exercised a greater relative influence than tiller angle and leaf length. Tiller number thus appeared to be more important to determining Y_{DOM} than tiller angle and leaf length. In smooth bromegrass Tan et al. (1977) found by means of a path coefficient analysis that, after leaf area, tiller density was the second most important factor controlling forage yield. Tiller density showed a very high genotypic correlation with dry-matter yield.

Selection of plants with a high tiller number will therefore increase dry-matter yield, which agreed with the conclusion reached in Section 2.2.3, that selection towards high tiller density would compensate the loss in yield caused by selection for high D_{vitro} through low tiller weight and short tiller length.

2.4 INTER-VARIETAL VARIATION

2.4.1 Material and methods

Eight experimental varieties of setaria (K 7422, K 7424, K 7428, K 7432, K 7438, K 7439, K 7447 and K 7623) and Nandi I as standard variety were compared in a variety trial that consisted of a randomised block design with 4 replicates. On 18 Juni 1976, seed of each variety was broadcast by hand in plots of 4 x 5 m at a rate of 1.5 kg of germinating seeds per ha after mixing the seed with single super phosphate at the rate of 40 kg of phosphate per hectare.

The eight experimental varieties all originated from the spaced plant population of 4000 plants of Nandi I. The number of plants on which the varieties were based and the composition of the varieties were as follows:

- K 7422: the bulked polycross progeny of 28 plants, selected for earliness and growth vigour;
- K 7424: the bulked polycross progeny of 10 plants, selected for lateness and growth vigour;
- K 7428: the open pollinated progeny of an early plant with short and thin tillers;
- K 7432: the bulked polycross progeny of 6 plants, selected for earliness;
- K 7438: the bulked polycross progeny of 8 plants, selected for earliness and growth vigour;
- K 7439: the bulked polycross progeny of 8 plants, selected for lateness and growth vigour;
- K 7447: the bulked polycross progeny of 7 plants, selected out of K 7422 for lateness and growth vigour, and
- K 7623: the bulked polycross progeny of 10 plants, selected out of K 7422 on the basis of their progeny performance.

These 8 varieties formed part of the range of 32 experimental varieties that were developed in the breeding programme between 1971 and 1977. Some of the 8 varieties were included in this variety trial because they had proved their value during earlier testing, while others were evaluated for the first time.

On 20 July the trial was sprayed with 1 l of Oxytril in 300 l water per hectare to control *Ricandra* and *Commelina* species. Each plot was top-dressed with 40 kg of nitrogen per ha on 22 September 1976. The grass was cut back at a height of 10 cm on 18 November 1976.

After a cleaning cut on 4 April 1977 each plot was top-dressed with 40 kg of nitrogen per hectare. The quantity of nitrogen was set at this low level as the piece of land on which the trial was established had been utilized for seed production of the legume *Desmodium uncinatum* (Jacq.) DC. (silver-leaf desmodium) during the three preceeding years, which brought high soil fertility. Moreover, as the time of observation was to be eight-

een weeks, a large quantity of nitrogen would cause severe lodging, which could impair the accuracy of the yield determinations.

Sections of 1 x 1 m of undisturbed growth were cut at two-week intervals, beginning two weeks after the cleaning cut and covering a period of eighteen weeks of growth. In all 9 sections were cut. Within a section of one square meter of each variety a subsection of 0.18 square meters (Sample A) was first cut just above ground level, followed by the harvesting of the remaining part of the section at a height of 15 cm (Sample B). Samples A and B were weighed together to determine the yield of fresh material from each section. From Sample B, 500 g were dried in a forced-draught oven at 100 °C to determine the dry-matter content and D_{vitro}.

The following observations were taken from sample A:

- the number of tillers;
- the number of fully emerged flowering heads;
- the fresh weight of the stems (including leaf sheaths), leaf blades and dead material after hand separation.

Stems, leaves and dead material were dried and weighed, after which the % stem and tiller weight were determined.

2.4.2 Results

The sequence in time of head emergence could be established from the number of fully emerged heads in Sample A. As the number of heads were determined at two-week intervals, the data were interpolated to obtain the time of head emergence on a weekly basis. Variety K 7428 produced 10 heads per square meter three weeks after the cleaning cut and was designated as a very early variety. K 7422, K 7432 and K 7623 were early varieties with 10 heads per square meter four weeks after the cleaning cut - Nandi I belonged to this maturity class as well. K 7424 and K 7438 followed one week later (medium group), while K 7439 and K 7447 were late-heading, producing 10 heads per square meter 6 weeks after the cleaning cut.

For convenience, data are presented here for the average of the varieties of the four maturity groups. It has to be realised, however, that the groups consist of a varying number of varieties:

Very early - K 7428
Early - K 7422, K 7432 and K 7623
Medium - K 7424 and K 7438
Late - K 7439 and K 7447

Nandi I, the standard variety, belonged to the early group.

Table 16 gives Y_{DM}, D_{vitro} and % stem for each maturity group and Nandi I. Analyses of variance were calculated for the nine varieties for each regrowth period and for the means of the nine cuts. The varieties did not differ significantly for Y_{DM} at all regrowth periods, except for the fourteen weeks of regrowth, which showed a significant variety effect ($P < 0.05$). Differences between the means of the varieties were significant ($P < 0.05$) with two varieties of the medium group differing significantly from Nandi I. The very early variety showed an almost consistently lower dry-matter yield than

Table 16. Y_{DM}, D_{vitro} and % stem at different periods of regrowth. Between brackets: relative yields with Nandi I = 100.

Y_{DM} (g/m^2)

Maturity group	Period of regrowth (weeks)									
	2	4	6	8	10	12	14	16	18	Mean
Very early	111 (92)	263 (109)	391 (95)	483 (83)	883 (105)	820 (90)	741 (86)	815 (99)	905 (81)	601 (91)
Early	137 (113)	261 (108)	501 (122)	559 (97)	878 (105)	923 (101)	867 (100)	879 (107)	1069 (95)	675 (103)
Nandi I	121 (100)	241 (100)	411 (100)	579 (100)	839 (100)	913 (100)	865 (100)	820 (100)	1123 (100)	657 (100)
Medium	140 (116)	269 (112)	463 (113)	630 (109)	1008 (120)	1048 (115)	940 (109)	966 (118)	1244 (111)	745 (113)
Late	137 (113)	255 (106)	436 (106)	512 (88)	859 (102)	937 (103)	1018 (118)	946 (115)	1156 (103)	695 (106)
Mean	129	258	440	553	893	928	886	885	1099	675
Source of variation										
Varieties	NS	NS	NS	NS	NS	NS	*	NS	NS	*
Replicates	*	NS	NS	NS	NS	NS	NS	NS	NS	NS
% C.V.	20.7	18.2	19.9	19.4	15.3	15.7	13.1	15.5	15.6	8.2

D_{vitro}

Maturity group	Period of regrowth (weeks)									
	2	4	6	8	10	12	14	16	18	Mean
Very early	58.7	56.2	55.5	50.5	39.9	40.6	38.3	37.4	36.2	45.9
Early	56.8	56.5	52.9	49.6	42.6	41.0	38.5	34.9	33.8	45.2
Nandi I	57.6	57.5	54.7	51.8	43.2	45.0	37.5	35.8	33.7	46.3
Medium	55.8	56.4	53.8	49.7	42.4	41.4	37.4	34.5	33.7	45.0
Late	56.9	56.3	54.1	51.4	43.7	41.9	38.7	36.5	33.9	45.9
Mean	57.2	56.6	54.2	50.6	42.4	42.0	38.1	35.8	34.3	45.7
Source of variation										
Varieties	NS	NS	NS	NS	NS	*	NS	NS	NS	NS
Replicates	*	NS	NS	**	NS	NS	**	NS	NS	NS
% C.V.	6.0	2.2	4.2	4.0	6.4	7.6	4.4	10.1	7.3	3.1

% stem

Maturity group	Period of regrowth (weeks)									
	2	4	6	8	10	12	14	16	18	Mean
Very early	26.8	46.9	58.8	73.8	78.1	80.2	82.0	75.1	77.2	66.5
Early	31.2	46.6	59.5	68.1	73.3	78.6	77.4	72.1	72.7	64.4
Nandi I	26.1	44.1	48.6	69.5	73.6	75.1	80.7	75.3	74.9	63.1
Medium	30.8	47.5	52.9	67.8	72.0	76.7	77.0	75.9	72.5	63.7
Late	26.3	40.9	44.4	60.7	68.4	70.3	74.7	70.1	71.1	58.5
Mean	28.2	45.2	52.8	68.0	73.1	76.2	78.4	73.7	73.7	63.2
Source of variation										
Varieties	NS	NS	*	*	NS	NS	*	NS	NS	**
Replicates	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
% C.V.	20.3	12.6	13.9	7.9	5.4	7.9	5.1	4.8	5.9	36.9

* P < 0,05
** P < 0,01

During the first eight weeks of growth there was a linear increase in Y_{DM}. At ten weeks of regrowth Y_{DM} was overestimated, as the grass was lodged due to heavy rainfall, and this caused inaccuracies in sampling the fresh material. The grass harvested at twelve weeks of regrowth continued the linear increase set off by the early stages of growth. At fourteen and sixteen weeks the linear increase levelled off and stabilized, while at eighteen weeks the crop was lodged again due to a heavy downpour before sampling.

During none of the eight regrowth periods did the varieties show a significant difference for D_{vitro}, nor was there a significant difference in the means of the nine cuts. Ranges for D_{vitro} within the various regrowth periods amounted to 5.3% digestibility units maximally. The differences between the varieties were not consistent. D_{vitro} (Y) (mean of all varieties per regrowth period) dropped significantly ($P < 0.01$) at a rate linear with time (X = weeks after the cleaning cut) : $Y = -1.623X + 61.922$. D_{vitro} therefore decreased by 0.23% digestibility units per day. From eight to ten weeks D_{vitro} dropped sharply by about 8% units, which was probably caused by soil contamination of the samples due to heavy rainfall and lodging.

Differences between varieties for % stem were significant at six, eight and fourteen weeks regrowth and for the means of the nine cuts. From the onset of regrowth the late-maturing group of varieties had a lower proportion of stems than the other groups and differed significantly from Nandi I in the means of the nine cuts ($P < 0.01$). The very early variety differed more markedly from the other varieties at eight weeks and longer periods of regrowth. The difference between this variety and Nandi I was significant for the means of the nine cuts ($P < 0.05$). At older stages of growth, % stem dropped owing to the presence of more dead material consisting of leaves and stems, which was not fractioned.

The relationship between D_{vitro} and % stem was calculated for each variety for all periods of regrowth. All nine regression equations proved to be linear ($P < 0.01$). D_{vitro} at 40% stems could be determined from these equations and these values are presented in Table 17. The 40% stem stage was reached about four weeks after the cleaning cut, which corresponded to a dry-matter yield of approximately 2.5 tons per hectare, which is suitable for grazing. From Table 17 the higher digestibility of the very early-heading variety compared with the late-heading varieties, the varieties of the later ma-

Table 17. D_{vitro} at 40 % stems.

Maturity group	Variety	D_{vitro}	Mean D_{vitro}/group
Very early	K 7428	59.8	59.8
Early	K 7422	56.9	
	K 7432	56.4	
	K 7623	56.6	56.6
	Nandi I	56.1	56.1
Medium	K 7424	56.0	
	K 7438	56.4	56.2
Late	K 7439	53.8	
	K 7447	55.1	54.5

turity group in particular, is clear. The very early variety differed significantly ($P < 0.05$) from the other varieties.

Y_{DM} and D_{vitro} had a significant, negative correlation ($r = -0.958$ at 7 degrees of freedom) over the various regrowth periods for the means of the nine varieties. By extending the regrowth period Y_{DM} will increase, but for every 100 g/m^2 of dry matter produced, D_{vitro} dropped by 2.6% digestibility units over the period of observation covered by the present study.

As already mentioned, the eight experimental varieties were all derived from Nandi I. The two varieties of the medium group, that differed significantly from Nandi I in dry-matter yield, were K 7424 and K 7438. K 7424 was characterized by heavier but fewer tillers than Nandi I. K 7438 showed more and heavier tillers than Nandi I. The very early variety K 7428, which produced lower dry-matter yields than Nandi I, comprised plants with more, but finer tillers than Nandi I - this latter characteristic affected the dry-matter yield of K 7428 correspondingly.

2.4.3 Discussion

By cutting undisturbed growth at regular intervals, inter-varietal variation for D_{vitro} and Y_{DM} and their mutual relationship could be studied at equal times of regrowth and at the same morphological stage by interpolation. A comparison could thus be made between the results obtained under spaced-plant conditions as described in Section 2.2 and 2.3 and the results now obtained under sward conditions.

A striking difference between the D_{vitro} values found in the spaced plant population and in the variety trial is the far much smaller range in D_{vitro} of the latter.

D_{vitro} of the 121 plants varied by up to 10% digestibility units compared at the same morphological stage (Table 7), while the nine varieties displayed a range of 6% units at 40% stems (Table 17). The variability for D_{vitro} of the spaced plants was even greater per individual harvest. Comparison at the same time of regrowth showed that individual plants varied up to 19.6% digestibility units at nine weeks' regrowth (Table 13). The range in D_{vitro} of the individual varieties under sward conditions amounted to 5.3% units maximally within a regrowth period.

The plants that formed the base of the eight experimental varieties displayed a similar heading-time range as the 121 random plants that were studied in Sections 2.2 and 2.3. D_{vitro} of the eight varieties, compared at a comparable growth stage, was therefore expected to vary accordingly, but apparently the initially observed variability for D_{vitro} under spaced-plant conditions could not be repeated under sward conditions. The absence of a large genetic variation for D_{vitro} was expressed by the low heritability value of the swards, which was 0.06. Under spaced-plant conditions h^2_w was 0.75 (Table 9) and 0.25 (see Section 2.3.2). Concurrently, the range in time of head emergence of the eight varieties was less extreme under sward conditions than under spaced plant conditions.

Various authors have reported on the variability for D_{vitro} of plants under spaced conditions and their progenies under sward conditions.

In cocksfoot, high and low digestibility selections were made in families deriving

from crosses between genotypes of various origins (Breese & Davies, 1970). The first screening was based on observations made by Cooper et al. (1962) in sown boxes. Selection in the second and third cycles, was based on spaced-plant performance. Plants were compared in the year of seeding on a time basis, while in the first year after establishment, plants were compared at a comparable growth stage (ten days after head emergence) and their six weeks' aftermath. A marked change in the physiological and morphological characteristics of the two selections occurred. The high-digestibility selection (ten days after head emergence the selection showed 7% digestibility units higher D_{vitro} than the standard variety S 37), had a faster growth rate, an earlier date of heading, a greater stem width and a larger leaf than the low-digestibility selection (on average the low selection was 4.8% units lower than S 37).

The major difference in digestibility was caused by the stem digestibility rather than by differences in leaf digestibility (E.L. Breese, pers. comm.). Three varieties were developed out of the high-digestibility material which, when compared with the control variety S 37 and the low-digestibility selections, had lost their advantage in D_{vitro} under sward conditions. The competition under sward conditions apparently did not allow the expression of the high D_{vitro} value. Spacing experiments were conducted (A.C. Thomas, pers. comm.) as a follow-up in the field at spacings of 1.0 and 0.5 m, which only gave differences of 1-2% units, and in boxes, which gave a 7% unit difference at 30-cm spacing compared with broadcasting in the first cut, but no differences occurred in the second cut.

Kamstra et al. (1973) reported a similar case with smooth bromegrass, in which the expected differences between high and low digestibility selections could not be detected under sward conditions. Cristie (1977) in the same species, found that the variability for D_{vitro} was much less among the progenies in swards, than among the corresponding parents under spaced-plant conditions.

The observed difference between spaced-plant and sward performance might have been caused by the presence of a genotype × environment interaction under spaced-plant and sward conditions. Under spaced-plant conditions more light is intercepted, while more nitrogen and minerals are available underground than under closed-canopy conditions.

On the relationship between D_{vitro} and maturity at a comparable morphological stage, a similar conclusion could be drawn for the varieties as for the spaced plants: early-heading varieties had a higher D_{vitro} (Table 17), which agreed with an earlier reported varietal comparison between Nandi I, Nandi II and Nandi III (Van Wijk, 1976). It should be emphasized that the stems of the various varieties used for the varietal comparison in Table 17 differed in age. Early-heading varieties reached the defined percentage earlier than the late-heading varieties, thus giving rise to the differences in D_{vitro} for the reasons outlined in Section 2.2.3.

No definite picture emerged regarding the comparisons made at the same time of regrowth. The varieties did not show a correlation between D_{vitro} and maturity at the same time of regrowth, which agreed with earlier results obtained (Van Wijk, 1976).

Digestibility dropped during the sixteen-week period of observation 0.23% digestibility units per day. In Section 2.3.2 a drop of 0.30% units daily was reported during six weeks of observation. Over a fourteen-week period the daily decrease in digestibili-

ty of the three setaria varieties Nandi I, II and III amounted to 0.26% units (Van Wijk, 1976). Hacker & Minson (1972) found a drop of 0.23% digestibility units in a Nandi variety (it is not known whether Nandi I or Nandi II was utilized) over a period of four to twelve weeks, averaged over 2 years and 3 sites. These values are thus in close agreement. Reid et al. (1973) calculated a daily reduction in digestibility of 0.44% units in the Nandi (probably) I variety during a sixteen-week period. The data have been summarized in Figure 4, confirming the decrease in digestibility with time of a number of other tropical grasses referred to in publications of Milford & Minson (1968), Minson (1971a), Minson (1971b) and Reid et al. (1973).

Reid et al. (1973) compared the daily drop in digestibility of some cultivated tropical grasses (Congo signal grass, Rhodes grass, setaria and *Panicum maximum* Jacq. (Guinea grass)) with that of some temperate grasses (smooth bromegrass, cocksfoot, tall fescue, timothy and *Poa pratensis* L. (smooth-stalked meadowgrass)) and found that the daily drop was 0.31 and 0.22% units, respectively. They concluded that the changes in tropical and temperate grasses were similar. Thus, in spite of the less concentrated pattern of head emergence of tropical grasses and the lower level at which digestibility started off, the daily decrease was approximately equal for both grasses.

Minson (1971b) calculated from various in vivo experiments with tropical grasses that the daily rate of decrease in digestibility was about 0.1% units, which agreed with the value found in Section 2.2.2. Minson (1971b) compared the daily drop in in vivo digestibility of tropical grasses with that found by Minson et al. (1960) in temperate grasses where digestibility dropped with 0.5% units per day after the beginning of head emergence.

It should be emphasized that in the above-quoted comparisons of Reid et al. (1973) and Minson (1971b) the calculated drop in digestibility depends on the level at which digestibility starts off and on the duration of the comparison (see Fig. 4). No definite conclusions should therefore be drawn between tropical and temperate grasses as to a difference or similarity in a digestibility drop.

Figure 5 compares the varieties for dry-matter yield at a given digestibility level (D_{vitro} = 55%) on a time basis. The three early varieties showed considerable differences in dry-matter yield. Owing to its low productivity, the very early variety K 7428 reached the 55% level at its corresponding yield level much later than the medium varieties. The varieties of the late-heading group behaved almost the same way. Nandi I was the latest variety to reach the 55% level. On the basis of this figure, K 7422 and K 7438 could be recommended as they combined a high growth rate with a relatively high dry-matter yield and digestibility. But for a different farming system, the recommendation could go to variety K 7623 as this variety produced a high yield of dry-matter at the 55% level over a longer period of growth, thus ensuring the grazier a longer grazing period for his cattle on grass of this particular quality. However, these figures refer only to one cut at a particular time of regrowth, while for the farmer the total annual dry-matter yield and its distribution over the year is what matters. Perennial yield trials, cut at regular intervals, finally followed by grazing trials will ultimately assess the yielding ability and persistence of the variety.

The differences between varieties for Y_{DM} were greater than those observed for

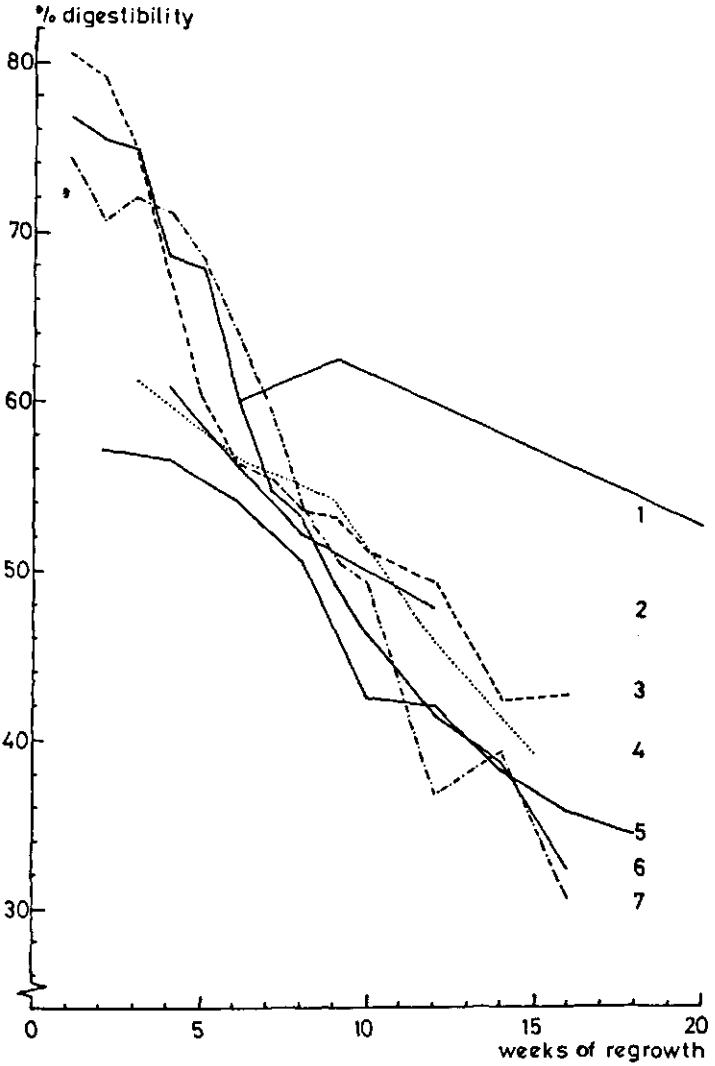

Fig. 4. The relationship between digestibility and maturity of some tropical grasses.
1. *Chloris gayana* (Milford & Minson, 1968)
2. *Setaria anceps* (Hacker & Minson, 1972)
3. *Panicum maximum* (Reid et al., 1973)
4. *Setaria sphacelata* (Van Wijk, 1976)
5. This study - data from Table 16)
6. *Chloris gayana* (Reid et al., 1973)
7. *Setaria sphacelata* (Reid et al., 1973)

D_{vitro} (Table 16), which agreed with the findings of the spaced plants (Table 13). One of the two varieties that differed significanty from Nandi I, that is K 7424, was also significantly different from Nandi I ($P < 0.05$) in Y_{DM} in a variety trial conducted at nine locations throughout Kenya over a period of three years, including four other experimental varieties of setaria (data not presented). This trial was cut regularly when approximately three tons of dry-matter per ha had accumulated. In the very early variety K 7428 a higher D_{vitro} was achieved, but Y_{DM} consequently dropped below the standard.

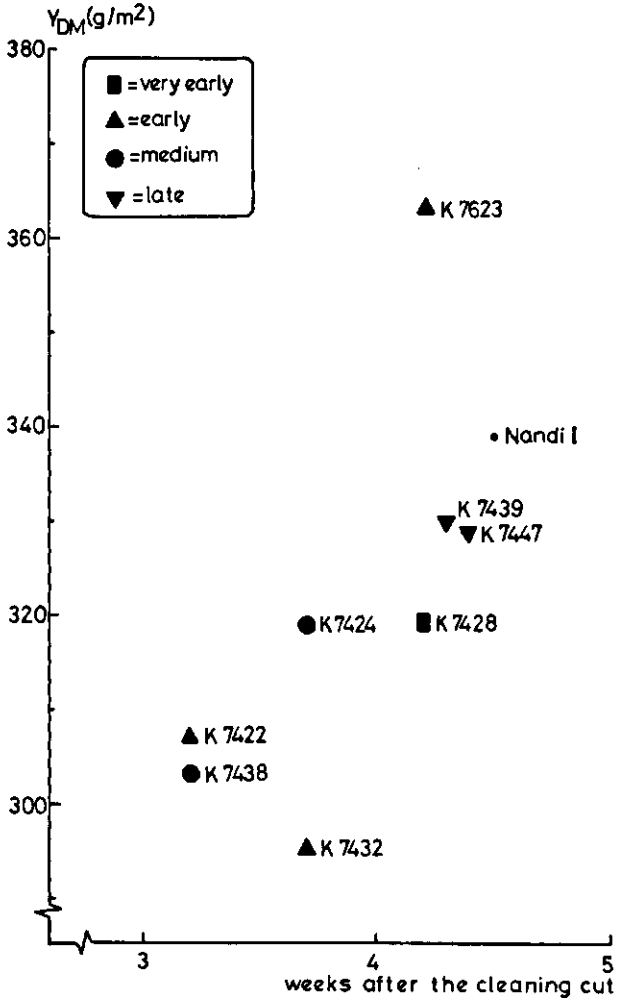

Fig. 5. Y_{DM} of 9 varieties at 55% D_{vitro}.

The other experimentals were bred aiming at a high growth vigour, which was obtained by means of an increased tiller number and tiller weight compared with Nandi I. D_{vitro} was hardly affected by the higher dry-matter yield and corroborating the final conclusion in Section 2.3.3, it can therefore be said that selection for Y_{DM} is the most effective way to increase Y_{DOM}.

2.5 THE PROSPECTS OF BREEDING FOR IMPROVED YIELD OF DIGESTIBLE ORGANIC MATTER

As the yield of digestible organic matter of plants and varieties is subject to continuous alteration during the growing season, it is of the utmost importance to define the basis of comparison between plants and varieties when selecting for improved digestibility and yield. Published results on digestibility improvement often do not mention the growth stage at which the comparison was made and the yield level at which the increase

of quality was achieved and are therefore less significant.

It is in this light that the following has to be viewed. Dent et al. (1967), considered a difference of 1.25% digestibility units between varieties within a species as of vital importance to the plant breeder, particulary if cumulative improvements of this magnitude could be achieved. Stobbs (1975) calculated from data of Minson (1971a and 1972) that an average increase in digestibility in tropical grasses of 4% could lead to an 8% increase in voluntary intake and 20% increase in digestible energy consumption, which should result in an increase of animal production by 40%. A high correlation between digestibility and intake was assumed. From various studies with temperate grasses, Lampeter & Schmeisser (1974) concluded that a relative increase in dry-matter digestibility of 2% would mean an increase of 400 kg of milk per cow per year. The growth stage at which these improvements would be achieved was not mentioned. Only Burton et al. (1967) clearly defined the stage which the relative increase of 12.3% in digestibility of a hybrid of Bermuda grass was achieved that is at two, three, four and six-week cutting intervals over a four-year period.

The expectations as to the effect of increased digestibility on animal performance were high, but the results of developing varieties of panmictic grass species of improved quality have been negative till now due to the fact that the differences in digestibility initially observed under spaced-plant conditions could not be maintained under sward conditions. Vegetatively multiplied and apomictic, spreading grasses offer a far greater possibility of fixing the selected increase in digestibility as varieties of these grasses consist solely of one genotype and also because their evaluation as single plants can be carried out under closed sward conditions (see Chapter 4).

Intra-varietal variation for D_{vitro} in setaria was strongly correlated with age when compared at a similar growth stage, as was inter-varietal variation but to a lesser extent. The variability for D_{vitro} was slight compared to the variation present for other plant characteristics. Within the same class of maturity the variation for D_{vitro} was even less and no specific morphological characteristic could be held responsible for the observed variation. In view of the results discussed in Section 2.2, selection for D_{vitro} among plants with different maturity seemed feasible, but a negative response in dry-matter yield was anticipated. When selecting plants with a high Y_{DOM} (see Section 2.3.2) only those were selected that had a higher tiller number and tiller weight than the average, while characteristics such as leaf width, leaf length and leaf number remained practically unchanged. Consequently, selection for Y_{DOM} seemed to be more efficiently applied by selecting for Y_{DM} rather than for D_{vitro}.

Selecting for Y_{DM} under spaced-plant conditions should, as for D_{vitro}, lead to a comparable improvement when tested under sward conditions and this will be discussed further in Chapter 4. It should be emphasized that the plants forming the base of the eight experimental varieties studied in Section 2.4, were all selected for a high degree of growth vigour. Comparison between spaced-plant and sward performance for Y_{DM} is therefore biased as the 121 plants were a random sample out of Nandi I, whereas the eight varieties were made apart of selected plants.

The results obtained with the high-digestible Bermuda grass variety Coastcross and the perennial ryegrass variety Mascot stand in contrast to the finding that selection

should be directed to an increase in Y_{DM}. The Coastcross variety produced 28% less dry-matter than its low-digestible parent Coastal Bermuda (Utley et al., 1974). The higher average live-weight gain per ha obtained with steers grazing Coastcross is therefore largely attributable to its higher digestibility, which amounted to 9.2% compared to Coastal Bermuda. It is doubtful, however, if the differences between the two varieties could be repeated to the same extent at a very high stocking rate.

The perennial ryegrass variety Mascot was selected out of S 23 for a higher dry-matter yield under spaced-plant conditions. Under sward conditions in a grazing experiment the variety yielded 4% less organic matter, but the live-weight gain of the animals grazing this variety was up by 14% compared to S 23 (Evans et al., 1979). The results were obtained from only one year's data. The higher individual gains on Mascot were partly attributed to a higher intake, but mostly to the greater efficiency of feed used by the animal. Preliminary investigations suggested that this was related to higher leaf and lower dead-material contents of Macot.

In spite of these last-named results, the prospects of breeding for digestibility by exploiting intra- or inter-varietal variation are not promising. It would seems more rewarding to introduce characteristics which act specifically on quality through hybridization with different ecotypes or species, as was done with Bermuda grass (Burton et al., 1967), pearl millet (Burton et al., 1969) and cocksfoot (Breese & Davies, 1975).

If spaced plants have to be compared for digestibility, plants can be best compared by collecting tillers of the same morphological stage at a clearly defined stage in their development. An advantage is that the plant can still be assessed for its seed-producing ability. The population of 121 plants has also been compared by cutting the whole plant at its time of head emergence (data not presented). However, by cutting the whole plant, inter-plant competition was raised, resulting in a strong stimulus to growth of the remaining plants. The late-heading plants therefore differed in morphological composition from what they would have been under competitive stress.

Cutting undisturbed growth at different periods of regrowth seems to be an effective way of comparing varieties with different growth patterns. By means of interpolation, varieties can then be compared at any given yield of dry-matter or level of digestibility, irrespective of growth stage and vice versa.

3 Variation for reproductive characteristics

3.1 INTRODUCTION

In North America numerous studies have been conducted on grasses during the 1950s to assess the potential for seed-yield improvement (Burton & DeVane, 1953; Lowe & Murphy, 1955; Raeber & Kalton, 1956 and Dewey & Lu, 1959). In European grass breeding major emphasis has been on selection for forage quantity and quality and only during the last two decades did breeding for seed yield receive greater attention (Griffiths, 1965; Lewis, 1966 and Bean, 1972).

The reason for this line of thinking may have been the low seed potential of the species under study in North America and the distinction made between earliness and lateness of head emergence of varieties, which has always been more pronounced in North-Western Europe than in America. Both types of varieties have a clearly defined role to play in grassland farming. Early-heading varieties are especially suited for conservation cuts because of their fast growth rate. Late-heading varieties, however, extend their vegetative growth to heading time over a longer period than early varieties, and therefore leave the farmer more time to utilize nutritious herbage for high-quality grazing.

Before the second World War major attention in grass breeding was focussed on the relation between maturity, growth habit and persistence. Under the influence of the work done at the Welsh Plant Breeding Station in the 1930s, earliness of heading was thought to be connected with an erect growth habit and low persistence, while later plants or varieties were characterized by a prostrate growth habit and high persistence. Early varieties had a higher seed-yielding ability than late-heading varieties. Breeding late-heading varieties was still regarded as ideal by Davies in 1960.

After the second World War grass breeding developed to the high levels of today. In the 1950s Dutch breeders collected material from old pastures in Holland and found that the correlation between earliness and low persistence could be broken (Lackamp, 1977). A whole range of varieties with varying maturity and persistence were developed, as is evident from Table 18. Breeding for seed yield didn't receive as much attention for fear of sacrificing the high herbage quality of the late varieties, though these yields were low. Moreover, as seed-growing techniques improved, seed production increased anyway.

The realisation that continuous breeding for lateness and leafiness could impair the economics of seed growing might explain why interest in breeding for increased seed yield came to the fore during the 1960s. Moreover, as the number of technically good grass varieties with slight differences in vegetative characteristics grew, the economics of grass-seed production ultimately decided the commercial succes of a variety. Consequently present varieties of perennial ryegrass entered on the Dutch Recommended List of Varieties no longer show a correlation between maturity and seed yield. A correlation coefficient

Table 18. Ground cover of different varieties of *Lolium perenne* L. (perennial ryegrass) (after Scheijgrond & Vos, 1960).

Varietal type	% cover	
	after 3 years' frequent mowing of pure swards	after 3 years' grazing of grass/clover mixture
Late, persistent	90	85
Late, moderately persistent	40	40
Medium late, persistent	90	75
Medium late, nonpersistent	5	5
Early, persistent	85	80
Early, nonpersistent	2	12

of 0.047 (19 degrees of freedom) was obtained between maturity and seed yield. The latter was averaged over three to six harvests taken from at least ten commercial fields of each variety (Anonymus, 1979). The range in maturity for the twenty-one varieties investigated varied from 10 May to 12 June.

The early European concept of grass breeding (the selection of leafy, late-heading varieties) was followed in Kenya (Bogdan, 1959), which was prompted by the stemmy appearance of tropical grasses as outlined in Chapter 1. Late-heading varieties of setaria and Rhodes grass were developed without much attention being paid to their seed-yield potential, already low in cultivated tropical grasses.

The factors determining seed yield can be divided into direct and indirect factors. The direct factors comprise:

- number of inflorescences;
- number of florets per inflorescence;
- number of florets which set seed (fertility);
- weight of individual seeds.

Indirect factors include spread in flowering time, lodging, seed retention, diseases and bird damage. Basic knowledge about the extent of variation available for each of these components within a species and their interrelationships has to be acquired before breeding for seed-yield improvement can be started.

Published results revealed that considerable variation is present for the four direct factors in grasses such as smooth bromegrass (Raeber & Kalton, 1956 and Knowles et al., 1970), Rhodes grass (Boonman, 1978a), tall fescue (Burton & DeVane, 1953; Bean, 1969 and Bean, 1972), *Panicum coloratum* L. (Kleingrass) (Hearn & Holt, 1969), timothy (Bean, 1972) and setaria (Boonman & Van Wijk, 1973). Heritabilities of the seed components in both the narrow and the wide sense varied to a great extent between the different grasses.

Fertility exerted the greatest influence on seed yield in smooth bromegrass (Lowe & Murphy, 1955) as found by fertility showing the highest correlation between seed yield and its components, and in crested wheatgrass and *Festuca pratensis* Huds. (meadow fescue) (Dewey & Lu, 1959 and Lewis, 1966 respectively) as determined from a path-coefficient

analysis of the seed components on seed yield.

A negative response in dry-matter yield when selecting for seed yield in tall fescue was expected by Burton & DeVane (1953). Schaaf et al. (1962) reported the absence of a significant relationship between forage and seed yield in crested wheatgrass, while Lewis (1966) and Knowles et al. (1970) found that selection for seed yield would not have adverse effects on forage yield in meadow fescue and smooth bromegrass, respectively. A positive trend in forage yield was observed by Knowles (1977) in five cycles of mass selection for seed yield in *Agropyron intermedium* (Host) Beauv. (intermediate wheatgrass). Knowles (1971) earlier concluded that selection for higher seed yields had shown more progress than selection for forage improvement in bromegrass, crested wheatgrass, intermediate wheatgrass and reed canary-grass. It should be emphasized that in these studies except in that of Lewis (1966), forage yield was determined at time of seed harvesting. A high number of culms would inevitably lead to a high forage yield due to the high dry-matter content of the stems. Lewis (1966), however, determined forage yield at anthesis and in October. The correlation between seed yield and forage yield per plant at anthesis was higher than in October, thus corroborating the foregoing.

Of the indirect factors, seed retention received most attention. McWilliam (1963) achieved a seed-yield increase of 60% compared to a widely grown commercial variety of bulb canary-grass by selecting for seed retention in an Argentinian variety. Bean (1965) selected plants from 50 clones of timothy on the basis of their seed-retaining ability, which yielded 30 to 45% more seed than the original varietal means.

Sown tropical grasses produce much less seed than temperate grasses, because of morphological and physiological characteristics.

Dirven et al. (1979) compared seed components of some tropical and temperate grasses as reported in the literature and concluded that the smaller number of fertile tillers per unit area is the main factor in the much lower seed yields of tropical grasses. The seed weight per inflorescence of tropical grasses was about the same as in temperate grasses.

Another group of factors in the low seed yields of tropical grasses concern impaired synchronization of flowering. In temperate grasses, daylength determines the time of heading of individual plants. In tropical grasses, the effect of photoperiodism has not yet been investigated thoroughly and it is often said that differences in daylength are unlikely to play an important role in the heading pattern of tropical grasses. However, marked effects have been reported to occur in some Gramineae, due to slight seasonal changes (Evans, 1964). Most tropical grasses are quantitative short-day plants, which means that inflorescence development is accelerated under short daylength conditions. Boonman & Van Wijk (1973) stated that plants do not produce heads until a minimum of herbage has accumulated. In Table 8 the positive, genotypic correlation between time of head emergence and leaf number is presented, which means that late-heading tillers possessed more leaves than early-heading tillers, thus contradicting Boonman & Van Wijk (1973) and showing that some response to photoperiodism or other effect might be involved. Irrespective of the reasons, cultivated tropical grass varieties display a prolonged head emergence (partly caused by the heterogeneity of the varieties) and, even within plants, head emergence is prolonged as each tiller may produce an inflorescence depending on its stage of development. Next to prolonged head emergence, extended flowering within inflorescences is held responsible

for the low seed yields (Boonman, 1971a). Moreover, the low tiller density results in a seed crop with open spaces, which will adversely affect head appearance.

The application of good crop husbandry techniques in seed production, such as adequate and timely top-dressing with nitrogen, narrow row width and the correct timing of harvesting increased seed yields considerably (Boonman, 1973b), although the absolute yield level was still low and very variable. The basic idea behind these measures was to increase the number of fertile tillers and to narrow the range in head emergence, thus favouring synchronization of flowering. However, these techniques would have an even higher response if applied to varieties with more uniform characteristics for seed components. Boonman & Van Wijk (1973) therefore assessed the amount of variation for seed yield and its components among eighteen selected clones of setaria and concluded that seed yield could be improved by breeding. Boonman (1972a) included % pure germinating seeds as an extra requirement of the germination because of the low viability of tropical grass seeds. Yields were then expressed as yield of pure germinating seed (Y_{PGS}) (see Appendix 1 for definitions).

The variation present for seed yield and some of its components within the spaced-plant population of 121 plants and the variation between varieties of setaria, are reported in the following sections.

3.2 INTRA-VARIETAL COMPARISONS OF UNREPLICATED PLANTS

3.2.1 Material and methods

Prior to the vegetative multiplication of the 121 plants which occurred in the spaced-plant population of 4000 plants of Nandi I in November 1973 as described in Section 2.2.1, measurements on seed yield and its components were carried out on the 121 unreplicated plants in the first crop of 1973.

The population of 4000 plants, including the 121 plants, was cut back and top-dressed with 100 kg of nitrogen per hectare on 27 April 1973. Time of head emergence of each plant was recorded. The inflorescences of each plant were harvested as described in Appendix 1. The following observations were made on the harvested flowering heads and the threshed seed:

- number of heads;
- head length of 25 heads;
- 1000-grain weight;
- yield of clean seed (Y_{CL});
- % germinating seeds (% GS);
- yield of germinating seed (Y_{GS}).

After harvesting, the whole plant was cut at 15 cm from ground level for the determination of its fresh weight.

From the recorded data the Y_{CL} and Y_{GS} per head were calculated. Simple correlation coefficients between the measured characteristics were calculated.

A path-coefficient analysis according to Dewey & Lu (1959) was carried out between seed yield as the dependent variable and head number, head length and 1000-grain weight as the independent variables.

3.2.2. Results

Table 19 gives the ranges, the means and the coefficients of variation of the various characteristics. The seed-production properties of forty-nine spaced plants of timothy, selected for high seed yield and presented by Bean (1972), are included in the same table. Within the setaria population of 121 plants, wide variation of the various characteristics occurred. Y_{CL} and Y_{GS} in particular showed divergent values as expressed by their high coefficients of variation. Head number, head length and 1000-grain weight of the setaria and timothy plants were approximately equal, but Y_{GS} per plant and per head of the two species differed to a very large extent, for which the low germination percentage of the clean seed of the setaria plants must be held responsible.

The simple correlation coefficients between the various seed characteristics and other plant characteristics are shown in Table 20. Y_{CL} per plant showed a positive, significant correlation with head number and head length and a significant negative correlation with 1000-grain weight and time of head emergence. Early-heading plants thus had a higher Y_{CL} than late-heading plants. The early-heading plants were further characterized by a larger number of lighter seeds than late-heading plants concerned in this study, which explains the negative correlation between Y_{CL} and 1000-grain weight.

The lower 1000-grain weight of the early-heading plants resulted in a lower germination percentage of the seed of these plants as expressed by the positive correlation between % GS and time of head emergence. A high Y_{CL} will therefore not necessarily mean a high Y_{GS} - the correlation coefficient between Y_{CL} and % GS was -0.090. Because of these relationships, time of head emergence and Y_{GS} did not show any correlation.

The same explanation could be given for the negative correlation between time of head emergence and Y_{CL} per head and the positive correlation between time of head emergence and Y_{GS} per head - the latter correlation coefficient was not significant however.

There was no correlation between head length and Y_{GS} per plant and per head, while

Table 19. The ranges, the means and the coefficients of variation (% CV) of the 121 unreplicated setaria plants and the means of 49 plants of *Phleum pratense* L. (timothy) after Bean (1972).

Characteristic	121 setaria plants			49 timothy plants
	range	mean	% CV	mean
Head number	42-377	211	29.3	212
Head length (cm)	7-25	17	17.5	13
1000 grain weight (mg)	192-709	467	18.8	430
Y_{CL} per plant (g)	0.1-33.4	6.5	74.4	-
Y_{CL} per head (mg)	1-167	30	70.2	-
% GS	0-46.7	20.9	61.5	-
Y_{GS} per plant (g)	0-5.6	1.3	92.2	36
Y_{GS} per head (mg)	0-18	6	85.6	184

Table 20. Simple correlation coefficients between seed characteristics, time of head emergence and fresh weight of the plant at seed harvest.

	Head number	Head length	1000-grain weight	Y_{CL}/plant	Y_{CL}/head	% GS	Y_{GS}/plant	Y_{GS}/head	Time of head emergence	Fresh weight of the plant
Head number	-	0.028	-0.251**	0.390**	-	0.124	0.414**	-	-0.425**	0.693**
Head length		-	-0.168	0.227*	0.226*	-0.123	0.097	0.104	-0.332**	0.171
1000 grain weight			-	-0.358**	-0.300**	0.594**	0.155	0.215*	0.584**	-0.271**
Y_{CL}/plant				-	-	-0.090	-	-	-0.281**	0.480**
Y_{CL}/head					-	-0.131	-	-	-0.205*	0.244**
% GS						-	-	-	0.407**	0.066
Y_{GS}/plant							-	-	0.068	0.391**
Y_{GS}/head								-	0.148	0.187*
Time of head emergence									-	-0.311**
Fresh weight of the plant										-

* $P < 0.05$
** $P < 0.01$

head length and Y_{CL} per plant and per head showed a significant positive correlation. The first relationship arose out of the negative relation between Y_{CL} and 1000-grain weight on the one hand, and the positive relationship between 1000-grain weight and % GS on the other.

A striking feature in the spaced-plant population was the positive and significant correlation between seed yield and fresh weight of the plant at time of seed harvesting. Greater fresh weight of plants went hand-in-hand with a larger number of heads carrying more but lighter seeds than did plants of lower fresh weight. A similar correlation between time of head emergence and fresh weight as reported earlier (Table 8) was observed in this study.

Path coefficients were calculated between seed yield and head number, head length and 1000-grain weight and are given separately in Table 21 for Y_{CL} and Y_{GS}. The partitioning of Y_{CL} and Y_{GS} into direct and indirect effects did not further elucidate the rela-

Table 21. Path coefficients for Y_{CL} and Y_{GS}.

Y_{CL} vs head number	
Direct effect	0.323
Indirect effect via head length	0.005
Indirect effect via 1000-grain weight	0.062
	r = 0.390
Y_{GS} vs head number	
Direct effect	0.485
Indirect effect via head length	0.004
Indirect effect via 1000-grain weight	-0.075
	r = 0.414
Y_{CL} vs head length	
Direct effect	0.176
Indirect effect via head number	0.009
Indirect effect via 1000-grain weight	0.042
	r = 0.227
Y_{GS} vs head length	
Direct effect	0.133
Indirect effect via head number	0.014
Indirect effect via 1000-grain weight	-0.050
	r = 0.097
Y_{CL} vs 1000-grain weight	
Direct effect	-0.248
Indirect effect via head number	-0.081
Indirect effect via head length	-0.029
	r =-0.358
Y_{GS} vs 1000-grain weight	
Direct effect	0.299
Indirect effect via head number	-0.122
Indirect effect via head length	-0.022
	r = 0.155
Unexplained Y_{CL}	0.863
Unexplained Y_{GS}	0.860

tionships, as has already been shown by the simple correlation coefficients given in Table 20. The greatest direct effect on Y_{CL} and Y_{GS} was exerted by the number of heads, followed by 1000-grain weight, while head length was of lesser importance. The direct effect of 1000-grain weight acted on Y_{CL} and Y_{GS} in opposite directions for the reasons outlined above. The positive effect of 1000-grain weight on Y_{GS} was masked by the negative indirect effect of 1000-grain weight via head number - the correlation coefficient between these two characteristics being significantly negative. A high number of heads apparantly had a negative effect on seed size, but this was closely interrelated with time of head emergence.

3.2.3 Discussion

Within the population of the 121 plants of setaria a wide variation occurred with regard to seed yield and its components (Table 19). Early-heading plants had a significantly higher Y_{CL} than late-heading plants, but Y_{GS} was the same for all maturity groups (Table 20).

The higher Y_{CL} of the early plants was due to the higher number of heads of early plants compared with late-heading plants; head number had the largest direct influence on Y_{CL} (Table 21). An increase in Y_{CL} by selecting early plants will therefore be largely due to an increase in the size of the reproductive system rather than to improvement in its efficiency. Selection towards earliness (and consequently Y_{CL}), however, does not necessarily mean that Y_{GS} is increased simultaneously because of the absence of a correlation between % GS and Y_{CL}.

Y_{CL} and % GS were influenced by seed size, as expressed by the significant correlations of the first two characteristics with 1000-grain weight (Table 20), which resulted in the absence of a correlation between % GS and Y_{CL}. High clean seed yields comprised a greater number of small grains than the low yields, which affected % GS and Y_{GS} adversely. Early-heading plants in particular were characterized by lighter seeds than late-heading plants and it is open to doubt whether this is an inherent characteristic of these plants or is caused by environmental influences such as the time of harvesting.

Boonman (1973a) found that the later-harvested plots of three tropical grass varieties as calculated from their time of head emergence, had a higher 1000-grain weight and germination percentage than the earlier-harvested plots. Delaying harvest date increased seed shedding but, in a closed crop, 30% shedding could be allowed without impairing seed yield as it is the empty spikelets that are shed early (Boonman, 1975b). The harvesting of the spaced plants was carried out approximately seven weeks after IHE as this was found to be the optimum harvest time (Boonman, 1973a). But in view of the high correlation between time of head emergence and 1000-grain weight and % GS, early-heading plants might have been harvested too early, when their seeds had not yet fully matured. On the other hand, the significant negative correlation between head length and time of head emergence and the negative correlation between head length and 1000-grain weight do suggest that seed size is related to time of head emergence.

As already mentioned in Chapter 1, setaria resembles the temperate grass timothy and some comparisons on the seed-yielding ability of the two grasses can be made, though the

basis of comparison is entirely different for each of the two species. Compared to other temperate grasses, such as perennial ryegrass the fertile tiller density of setaria is very much lower (Dirven et al., 1979). These values did not differ so markedly for setaria and timothy, nor did 1000-grain weight and head length. The great differences in seed yield were caused by the low seed setting and viability of the seeds of setaria, influenced by the poor synchronization of the action of the seed components as outlined in Section 3.1.

The relationship between seed yield and fresh weight will be discussed in Section 3.3.3.

3.3 INTRA-VARIETAL COMPARISONS OF REPLICATED PLANTS

3.3.1 Material and methods

Apart from the intra-varietal variation for seed yield and its components as reported in Section 3.2, variation for seed yield was also studied in the spaced-plant population of the 121 plants described in Section 2.2.1, the experimental lay-out and crop husbandry techniques of which have been given in the same section. After recording the characteristics described in Section 2.2.1 and the removal of the 15 tillers per plant in order to establish the relationship between D_{vitro} and the various plant characteristics in the three crops in 1974 and 1975, the plants were allowed to produce seed.

The inflorescences of each plant were harvested approximately seven weeks after IHE as described in Appendix 1. The following observations were made on the harvested flowering heads and threshed seeds:

- number of heads;
- yield of clean seed (Y_{CL});
- % germinating seeds (% GS);
- yield of germinating seeds (Y_{GS}).

Y_{CL} and Y_{GS} per head were calculated from the recorded data. Of the various seed components only head number was recorded because this characteristic emerged as having the greatest direct effect on seed yield (Table 21).

At seed harvesting, the whole plant was cut at a height of 15 cm to determine its fresh weight. This characteristic has already been included in processing the data in Sections 2.2 and 2.3.

Spikelets affected by *Tilletia echinosperma* Ainsworth (bunt) were separated mechanically from the clean seed on a "Brabant" clipper for the two crops of 1975 and weighed per plant.

The measurements carried out in 1974 and 1975 were summed per entry and per replicate and analyses of variance of head number, Y_{CL} per plant, Y_{CL} per head, % GS, Y_{GS} per plant and Y_{GS} per head were carried out according to the model presented in Section 2.2.1. The analysis of covariance between these characteristics, except % GS and those dealt with in Section 2.2, were calculated in accordance with the same model. In both analyses observations were corrected for blocks, except for % GS, which was treated as being derived from plants in a randomised block design. These calculations were made according to the least squares method of Harvey (1976).

As % GS covered a wide range of values (from 0.6 to 74.5%), germination percentages were transformed according to Steel & Torrie (1960) into $\sqrt{\%GS + \frac{1}{2}}$. The transformed data approached a normal distribution.

Heritabilities in the wide sense on an individual plant basis of head number, Y_{CL} per plant, Y_{CL} per head, % GS, Y_{GS} per plant and Y_{GS} per head were calculated as outlined in Section 2.2.1. The coefficient of the genetic component of variance for % GS which was not analysed in a lattice design amounted to 3. The genotypic and phenotypic correlation coefficients were calculated as presented in Section 2.2.1.

The repeatabilities of head number, Y_{CL} per plant, % GS and Y_{GS} per plant were determined from the totals of the 3 replicates per harvest as defined in Section 2.2.1.

The means of the characteristics of the three crops measured in Section 2.2.1 and head number (all characteristics corrected for block effects) were treated as the independent variables in a multiple regression analysis, in which Y_{CL} and Y_{GS} per plant were the respective dependent variables. The best-predicting independent variables were selected by the method of Daniel & Wood (1971) which is described in Appendix 2.

3.3.2 Results

Table 22 gives the range, the coefficients of variation, the repeatability and the heritabilities in the wide sense on an individual-plant basis of head number, % GS and seed yield per plant and per head.

The population of 121 plants displayed a wide range in values of these characteristics and the differences between the plants for these characteristics were significant ($P < 0.01$). Y_{GS} in particular had a high coefficient of variation, which was calculated from the analysis of variance, indicating large replicate-to-replicate variation. The repeatability of head number, % GS and Y_{GS} per plant was negative, due to the large differences between harvests. The mean Y_{GS} of the three crops were 214, 1312 and 556 mg, respectively. Y_{CL} per plant, however, was not affected as much as the other characteristics by seasonal differences in view of its relatively high repeatability. % GS had a low heritability, while that of the other properties was high. The repeatability of Y_{CL} per head was the same as that of Y_{CL} per plant, but the repeatability of Y_{GS} per head was higher than that of Y_{GS} per plant, which pointed to the fact that the seed weight per inflorescence was less affected than Y_{GS} per plant by season-to-season differences.

Table 22. Ranges (means of 3 replicates of 3 harvests), coefficients of variation (% CV), repeatability (R) and heritabilities in the wide sense on an individual plant basis (h^2_w).

Charateristic	Range	Mean	% CV	R	h^2_w
Head number	37-241	129	21.7	-0.08	0.61
Y_{CL} per plant (g)	0.2-10.0	3.8	34.2	0.27	0.64
Y_{CL} per head (mg)	4-81	29	28.6	0.27	0.62
$\sqrt{\%\ GS + \frac{1}{2}}$	1.10-7.82	3.90	28.7	-0.01	0.13
Y_{GS} per plant (g)	0.1-2.5	0.7	68.7	-0.03	0.43
Y_{GS} per head (mg)	3-24	4	64.2	0.16	0.41

Tabel 23. Genotypic (r_g) and phenotypic (r_{ph}) correlation coefficients with head number, Y_{CL} and Y_{GS}.

Characteristic	Head number		Y_{CL} per plant		Y_{CL} per head		Y_{GS} per plant		Y_{GS} per head	
	r_g	r_{ph}	r_g	r_{ph}	r_g	r_{ph}	r_g	r_{ph}	r_g	r_{ph}
Tiller number	0.700	0.624	0.569	0.464	0.247	0.171	0.489	0.343	0.216	0.126
Time of head emergence	-0.485	-0.487	-0.236	-0.314	-0.021	-0.124	0.097	-0.054	0.285	0.055
Tiller angle	-0.270	-0.188	-0.124	-0.158	0.049	-0.072	-0.161	-0.140	-0.006	-0.071
Tiller length	0.283	0.267	0.487	0.336	0.368	0.217	0.504	0.349	0.374	0.252
Leaf number	-0.166	0.010	0.044	0.046	0.164	0.061	0.177	0.139	0.243	0.146
Leaf width	-0.110	-0.066	0.317	0.205	0.489	0.327	0.302	0.132	0.396	0.181
Leaf length	0.104	0.112	0.341	0.273	0.344	0.252	0.239	0.171	0.210	0.146
Stem diameter	-0.213	-0.198	0.219	0.081	0.446	0.252	0.227	0.051	0.356	0.140
Tiller weight	-0.070	-0.026	0.418	0.242	0.569	0.565	0.493	0.282	0.336	0.311
Fresh weight of the plant	0.610	0.573	0.786	0.631	0.594	0.420	0.617	0.401	0.404	0.242
Head number	-	-	0.634	0.600	-	-	0.286	0.308	-	-

Table 24. Multiple regression with $^{10}\log Y_{CL}$ and $^{10}\log Y_{GS}$ as dependent variables.

Full equation: $^{10}\log Y_{CL}$ *dependent variable*

Variable	Partial regression coefficient	t-value	Relative influence
Tiller number	0.0002	0.9	0.09
Time of head emergence	- 0.0617	2.4	0.20
Tiller angle	0.0085	0.6	0.04
Tiller length	- 0.0045	1.0	0.09
Leaf number	- 0.0025	0.7	0.06
Leaf width	0.0325	1.1	0.08
Leaf length	0.0006	0.1	0.00
Stem diameter	- 0.0883	0.7	0.06
Tiller weight	0.0157	1.2	0.18
Fresh weight of the plant	0.0028	2.9	0.43
Head number	0.0013	1.4	0.16
Constant	1.0255		

$F^{11}_{109} = 14.8^{**}$

Residual mean square = 0.0401
Squared multiple correlation coefficient = 0.599

Subset equation: $^{10}\log Y_{CL}$ *dependent variable*

Time of head emergence	- 0.0559	3.1	0.18
Fresh weight of the plant	0.0041	10.9	0.64
Constant	2.0699		

$F^{2}_{118} = 78.7^{**}$

Residual mean square = 0.0397
Squared multiple correlation coefficient = 0.571

Full equation: $^{10}\log Y_{GS}$ *dependent variable*

Variable	Partial regression coefficient	t-value	Relative influence
Tiller number	0.0008	2.6	0.32
Time of head emergence	- 0.0095	0.4	0.03
Tiller angle	0.0172	1.1	0.08
Tiller length	0.0087	1.8	0.18
Leaf number	- 0.0077	2.1	0.19
Leaf width	- 0.0138	0.4	0.04
Leaf length	- 0.0145	1.2	0.11
Stem diameter	0.0176	0.1	0.01
Tiller weight	0.0213	1.6	0.26
Fresh weight of the plant	0.0016	1.6	0.27
Head number	0.0006	0.7	0.08
Constant	- 0.0031		

$F^{11}_{109} = 12.0^{**}$

Residual mean square = 0.0434
Squared multiple correlation coefficient = 0.547

Subset equation: $^{10}\log Y_{GS}$ *dependent variable*

Tiller number	0.0004	1.7	0.17
Tiller length	0.0095	2.6	0.20
Fresh weight of the plant	0.0024	3.3	0.41
Head number	0.0005	0.8	0.07
Constant	- 0.4073		

$F^{4}_{116} = 31.3^{**}$

Residual mean square = 0.0432
Squared multiple correlation coefficient = 0.519

** $P < 0.01$

The highest genotypic and phenotypic correlation coefficients with both Y_{CL} and Y_{GS} per plant were shown by the fresh weight of the plant at seed harvest (Table 23). The same holds true for the genotypic correlation coefficient between fresh weight and seed yield per head. The number of heads showed a high correlation with Y_{CL}, but the correlation with Y_{GS} was not as strong. The number of tillers, as determined three weeks after the cleaning cut, showed a high genotypic correlation with both Y_{CL} and Y_{GS} - the high correlation between tiller number and head number has to be considered in this respect as well. Early-heading plants had a higher yield of clean seed per plant than late-heading plants, while there was no relation between Y_{GS} and maturity.

The correlations calculated on a per-plant and a per-head basis generally agreed, except for time of head emergence. Plants of all maturity groups had a similar Y_{CL} per head, while heads of late-heading plants had a higher Y_{GS} per head.

The results of the multiple regression analysis are shown in Table 24. The scatter diagram of the residuals versus the fitted y-values revealed that the scatter of residuals depended on the magnitude of y for both Y_{CL} and Y_{GS}. Therefore the dependent variables were transformed by taking the common logarithm of Y_{CL} and Y_{GS}. An even distribution of the residuals around the zero line was then obtained. The standard error estimated from near neighbours for Y_{CL} and Y_{GS} was 0.18 and 0.19, respectively and did not differ markedly from the standard error of 0.20 and 0.21 of the full equation.

Time of head emergence and fresh weight of the plant were the principal determinants of the clean seed yield. Both characteristics occurred in the basic set which was finally selected at $P = 3$ and $C_p = 2.0$ and accounted for 57% of the variation observed in Y_{CL}. The equation, consisting of time of head emergence, leaf width, fresh weight and head number, had the lowest residual mean square, but the P and C_p values varied considerably. The greatest influence on Y_{GS} was exerted by tiller number, tiller weight and fresh weight of the plant. The final subset equation, containing tiller number, tiller length, fresh weight of the plant and head number, was chosen at $P = 5$ and $C_p = 4.6$.

In the first crop of 1975 the weight of the spikelets affected by bunt amounted to 3.7% of the clean-seed weight of all plants together. In the second crop of the same year the diseased spikelets came to 57% of the clean-seed yield. The relationships between yield of clean seed, bunt and time of head emergence are shown in Table 25. Late-heading plants were more seriously affected by bunt than early-heading plants in the second crop, whereas in the first crop the effect was negligible.

Table 25. Partial correlation coefficients between Y_{CL}, amount of bunt and time of head emergence in 1975.

	First crop	Second crop
Time of head emergence - amount of bunt, Y_{CL} fixed	- 0.055	0.382**
Time of head emergence - Y_{CL}, amount of bunt fixed	- 0.326**	- 0.665**
Y_{CL} - amount of bunt, time of head emergence fixed	0.313**	0.707**

** $P < 0.01$

3.3.3 Discussion

In agreement with the results obtained in Section 3.2 the population of 121 plants evinced a wide variation in Y_{CL} and Y_{GS} per plant and per head (Table 22). Early-heading plants had a higher Y_{CL} than late-heading plants (r_g = -0.236), while Y_{GS} was approximately equal for all maturity classes (r_g = 0.097) (Table 23). Both Y_{CL} and Y_{GS} showed very high genotypic correlations with the fresh weight of the plant as measured at seed harvest (Table 23). Time of head emergence and fresh weight were the most influential variables of $^{10}\log Y_{CL}$; fresh weight appeared in the finally selected subset equation of $^{10}\log Y_{GS}$ (Table 24).

The results obtained in this study and those reported in Section 3.2 clearly indicated that the total overground biomass produced by a plant was a reflection of its reproductive capacity. Closely correlated to fresh weight was bulk density as calculated in Section 2.2.3 (r_g = 0.871, data not presented), which was a clear measure of plant size. Plants with a large fresh weight were therefore large and were further characterized by a high head number, as is evident from the strong correlation between these two characteristics (r_g = 0.610) (Table 23). The higher seed yield per plant of plants with a higher fresh weight was thus caused by an increased number of reproductive tillers.

The time of head emergence of a plant is determined by the ten heads that have emerged in a specific week. Large plants with a high tiller number might possibly reach the stage of 10 fully emerged heads earlier than sparse-tillering plants because of the larger number of tillers. The genotypic correlation between time of head emergence and tiller number was small, however (r_g = -0.169, Table 8) and it could be that this assumption was not true for all plants. The correlation between time of head emergence and head number was larger (r_g = -0.485, Table 23).

Not only did the number of reproductive tillers of large plants cause a high seed yield, but the seed yield per head of these plants was also higher than that of smaller plants, as is evident from the significant correlations between fresh weight and Y_{CL} and Y_{GS} per head (Table 23). Large plants had a lower 1000-grain weight than small plants, as is shown by the negative correlation between fresh weight and 1000-grain weight in Table 20, while the positive correlation between fresh weight and head length was not significant. The higher seed yield of large plants comprised a higher number of lighter seeds per unit head length than that of small plants.

In view of the foregoing and of the high correlations between fresh weight and Y_{DOM} at 3 periods of regrowth (Table 15), it is expected that selection for seed yield will not have adverse effects on forage yield. Moreover, fresh weight of the plant showed a very strong correlation with growth vigour, which was rated visually on a 1-5 scale (5 representing the greatest vigour) for the 121 plants when the earliest plants had reached their IHE (r = 0.933, 119 degrees of freedom) (data not presented).

A similar relationship between plant size and seed yield was reported in the temperate grass crested wheatgrass by Dewey & Lu (1959). Through a path-coefficient analysis, plant size was found to have the second largest direct influence on seed yield; fertility exerted the greatest influence.

It should be emphasized here that the relationship between plant size and seed yield was under spaced-plant conditions, which does not necessarily mean that the same relation-

ships exist in a closed-crop canopy for large-scale seed production.

Selection of early-heading, vigorous plants will greatly improve Y_{CL}, but will not automatically lead to increased Y_{GS}. The simple correlation coefficients between Y_{CL} per plant and % GS were -0.303, -0.010 and 0.077 for the three harvests, respectively (data not presented), while for the unreplicated plants this correlation, as reported in Section 3.2, was -0.090 (Table 20). This relationship was reported earlier for spaced plants of setaria (Boonman & Van Wijk, 1973) and was encountered in selected populations of Rhodes grass as well (Boonman, 1978a and 1978c).

As already pointed out in Section 3.2.3 there was in fact a significant, positive correlation between time of head emergence and % GS. Simple correlation coefficients between these two characteristics for the three harvests of 1974 and 1975 were -0.161 (NS), 0.393 ($P < 0.01$) and 0.185 ($P < 0.05$) respectively, indicating the tendency of late-heading plants towards a higher % GS than early-heading ones.

In addition to the explanation given in Section 3.2.3 for the lower % GS of early-heading plants, the higher % GS of late-headers might have been caused by the adverse effect on germination of the larger number of heads of the early plants. This was evident by the much lower genotypic correlation between head number and Y_{GS} than that between head number and Y_{CL} (Table 23). The correlation coefficients between head number and % GS for the three crops, however, were 0.005, 0.013 and 0.0003, respectively (data not presented), while the correlation between these two characteristics reported in Section 3.2 was non-significant as well (Table 20). Boonman (1972a) found in Nandi II that a high head number, when increased by a high nitrogen gift, led to a decrease in % GS, particularly at wide row width. The high nitrogen level was further associated with an increased head length (Boonman, 1972a). Early-heading plants were also characterized by longer heads than late-heading plants (Table 20), which might have led to a prolonged flowering and reduced seed setting per head, analogous to the lengthening of the heads because of the high nitrogen level. The correlation coefficient between head length and germination percentages was negative, but not significant (Table 20).

The relative influence of head number on Y_{CL} was greater than that of tiller number on Y_{CL} (Table 24), while for Y_{GS} the reverse took place - the influence of tiller number was greater than that of head number. In a multiple regression the contribution of one characteristic to the explanation of the dependent variable cannot be considered without taking into account the mutual association with the other independent variables.

Therefore, as the genotypic correlation between tiller number and Y_{CL} and Y_{GS} per plant did not differ to a very great extent and the correlation between tiller number and Y_{CL} and Y_{GS} per head was similar, the reversal of the relative influence of head and tiller number must have been due to the much lower genotypic correlation between head number and Y_{GS} per plant compared to that with Y_{CL} per plant. The reasons for this lower correlation have been stated earlier.

Selection for increased seed yield per plant will result in plants with a higher number of flowering heads. The necessary compromise between head number and % GS, might be found, as a next step, by selecting plants with a rapid, simultaneous head emergence and close matching of heading dates.

The higher number of heads can affect herbage quality and persistence. In itself,

increased stemminess may perhaps not impair herbage quality at very early stages of growth as very young stems can be of higher digestibility than leaves (Van Wijk, 1976). At later stages the higher stem percentage will have a negative effect on digestibility. R.P. Knowles (pers. comm.) did not find digestibility consistently affected as the result of selecting for seed yield in smooth bromegrass. On average, Nandi I had twice as many heads as Nandi III at optimum harvest time (Table 2), but no differences could be detected in persistence between the two varieties in a variety trial that was cut weekly at 5 cm length during a period of three years (data not presented).

The heritabilities (Table 22) were below the values reported by Boonman & Van Wijk (1973), which were only based on one year of observations and on clonal means. All characteristics, except % GS, displayed a high heritability, so that mass selection seems justified. In Rhodes grass, Boonman (1978a) too, found that % GS had a very low heritability and that the improvement of seed setting in tropical grasses by mass selection is apparently difficult.

The higher incidence of bunt in late-heading plants in the second crop of 1975 supported selection for earliness when breeding for seed yield. Bunt did not seriously affect seed yield in the first crop of 1975, but the damage it caused in the second crop was far more severe. Boonman (1972c) discussed the advantages of having an early first crop in view of the lesser occurrence of bunt compared to late crops.

3.4 INTER-VARIETAL VARIATION FOR SEED YIELD

Boonman (1971b) determined the major seed characteristics of Nandi I and Nandi III, as summarized in Table 2. Nandi II can be assumed to be intermediate between Nandi I and Nandi III (Boonman & Van Wijk, 1973).

From Table 2 it is evident that the early-heading variety Nandi I produced twice as much pure germinating seeds as the late-heading variety Nandi III. The yield per inflorescence was almost equal in both varieties, however. The higher Y_{GS} of Nandi I could therefore be largely explained by the larger number of flowering heads in Nandi I compared to Nandi III.

During 1970, 1971 and 1972 the spaced-plant populations of Nandi I and Nandi II, each consisting of 4000 plants (Chapter 1) were scored for time of head emergence and growth habit. For the latter characteristic all plants were classified as tall, flat or poor, at Week 1 (data not presented).

Nandi II showed a more concentrated head emergence than Nandi I. The medians of time of head emergence differed approximately by one week between the two varieties. In growth habit Nandi II differed from Nandi I in the higher proportion of short plants and the smaller number of flat, open-centred plants, which resulted in Nandi II being more uniform for plant type. The rejection of plants with an open centre, which was thought to suppress herbage productivity, was one of the major breeding objectives in developing Nandi II (Bogdan, 1965). A more uniform variety was thus obtained.

Though Nandi II possessed characteristics calculated to have a positive effect on the synchronisation of flowering, thus favourable to seed production, no improvement in this characteristic was in fact achieved. The positive effect of uniformity on seed production

was eliminated by the lower number of reproductive tillers, resulting in a lower seed yield than Nandi I.

The high tillering capacity of the other late variety Nandi III (Table 2), did not result in more generative tillers than in Nandi I. From temperate grasses it is known that a dense sward produces fewer fertile tillers. According to Sonneveld & Evers (1955) the production of fertile tillers in late heading varieties of species such as perennial ryegrass is suppressed by their dense-tillering capacity. The higher seed yield per ha of Nandi I compared with the dense-tillering variety Nandi III might have been due to the lower number of tillers per square metre of Nandi I, which allowed more space for reproductive tillers to develop. The open spaces in a seed crop of Nandi I due to the presence of poor plants with a low number of tillers could counteract the synchronization of flowering. But apparently natural selection within the ecotype of Nandi I established an equal balance between these factors.

4 Two methods of evaluating individual plants

4.1 INTRODUCTION

In grass breeding, initial selection is usually made from large source populations based on widely spaced plants. For tussock-forming species this means that the evaluation is done under conditions different from those under which the resulting variety will be ultimately used, that is sward conditions. The assumption is made that the differences detected between plants under spaced-plant conditions will be reproduced under the farmer's dense-sward field conditions.

The major disadvantage of the evaluation of spaced-plant populations is the absence of competitive stress: under spaced-plant conditions some plants can excell in dry-matter yield, whereas these plants would vanish in a sward. Spaced-plant populations, however, are a convenient means of scoring for characteristics such as time of head emergence, growth habit and resistance to diseases. As an open sward is more sensitive to cold, a spaced-plant population offers a better situation for selection for winterhardiness. England (1975) found that the ability of Italian ryegrass to survive into the second year after sowing can be assessed from spaced plants. Wide spacing exaggerates the plant's ability to survive long periods of drought. Spaced plants may also give too optimistic an impression about their seed-yielding ability compared to seed production in drilled fields.

The presence or absence of competition will influence the morphological composition of the plant, thus affecting characteristics like digestibility. In Section 2.4.3 the smaller range of setaria in D_{vitro} under sward conditions compared with spaced-plant conditions was discussed in conjunction with the results reported by Breese & Davies (1970) and Kamstra et al. (1973) on cocksfoot and smooth bromegrass, respectively - the initially observed differences between spaced plants for digestibility could not be reproduced under sward conditions.

Various other characteristics have been measured in numerous comparisons between spaced-plant performance and again at closer densities or under sward conditions. Conflicting results have been reported and summarized by Ribiero (1970). In general it was found that the prediction of sward yield based on the performance of widely spaced plants was unreliable.

During the initial stages of a breeding programme, however, seed is not readily available for experiments under sward conditions, so that the breeder still has to resort himself to individually spaced plants for their evaluation.

To approximate the desired situation of sward conditions for evaluation purposes, Lazenby & Rogers (1964) compared plant performance at different densities and concluded that the density at which the individual plants could still be isolated and the herbage still cover the ground completely, would give an evaluation comparable to that under

sward conditions. The major draw-back to this kind of evaluation is the difficulty, at close density, of distinguishing the various objects.

Van Dijk (1973) assessed single plants in a dense sward of another species. With this method individual plants could be screened under competitive stress while they were still recognizable. Van Dijk (1973) found a close correlation between spaced plants of timothy in monoculture and in a mixed culture with perennial ryegrass. The differences between the plants in the mixed culture were detected earlier and were found to be greater than in the monoculture. The accompanying grass in Van Dijk's experiment was a cross-fertilizing species and the timothy plants were therefore not subjected to the same aerial and root competition. Competition would be equal for all plants if the accompanying grass were to consist of an apomictic or vegetatively multiplicated species.

The foregoing applied especially to tussock-forming species. Species that spread by means of stolons or rhizoms, such as smooth-stalked meadow grass, Rhodes grass and Bermuda grass can only be evaluated as individual plants in little swards of their own. The problems of the tufted species outlined above are thus bypassed. However, tropical grasses have a much lower tiller density than temperate grasses (Dirven, 1977) and pastures of tropical, tufted grasses in Kenya rarely form closed swards, but consist of individually recognizable plants. Criticism on the assessment of herbage yield on spaced plants may therefore not be fully applicable to these grasses. In spite of this, a disadvantage of evaluating the material in swards is that the plant cannot express its full ability to vary because of the intensive competition. It was therefore decided to evaluate the 121 plants as described in Section 2.2.1 in a mixed culture according to Van Dijk (1973) and to compare the spaced-plant performance in monoculture with that in the mixed culture. The results are reported here.

4.2 MATERIAL AND METHODS

On 22 November 1973, clones of the 121 plants of setaria, as described in Section 2.2.1, were planted as single plants, one per square meter in a sward of Rhodes grass cv. Pokot that had been sown in 1972 at a rate of 1 kg PGS per hectare. The experimental lay-out was a triple lattice. Dead plants, amounting to 6% of the total number, were replaced by spare plants on 7 January 1974. Throughout the dry season the plants were irrigated.

The setaria plants and the Rhodes grass were both cut at a height of 10 cm on 15 May 1974, after which the setaria plants were top-dressed individually at a rate of 100 kg of nitrogen per hectare. The Rhodes grass did not receive fertilizer.

Cleaning cuts of both grasses at a height of 15 cm and top-dressings at 100 kg of nitrogen per ha on the setaria plants were carried out on 18 September 1974, 17 April 1975, 16 August 1975, 7 April 1976 and 17 July 1976 concurrently with the spaced plants in monoculture as described in Sections 2.2 and 2.3. The Rhodes grass was allowed to grow undisturbed after the cleaning cuts.

The observations made on each individual of the different crops are listed in Table 26. In 1976, the leaf percentage and that of dead material were assessed after 3, 6 and 9 weeks' regrowth from 50 randomly chosen plants in the mixed culture as described in Appendix 1. In the monoculture all plants were observed for these characteristics (see

Table 26. Characteristics recorded (x) in the mixed culture. The means and the coefficients of variation (% CV) of the characteristics and the rank-correlation coefficients (r_s) for each characteristic between the monoculture and the mixed culture. A = first crop; B = second crop.

Characteristic	Crops				Means per plant		% CV		r_s
	1974	1975 A	1975 B	1976	mono-culture	mixed culture	mono-culture	mixed culture	
Tiller number	x	x	x	-	401	195	31.0	39.0	0.65
Tiller angle	-	x	x	-	1.68	1.82	8.1	13.0	0.39
Time of head emergence (week)	-	x	x	-	3	4	30.8	36.0	0.63
Fresh weight of the plant (kg)	-	x	-	-	2.23	1.45	31.7	41.8	0.66
Number of heads	-	x	-	-	207	119	28.3	44.9	0.59
Y_{CL} (g)	-	x	-	-	5.19	0.53	61.6	66.1	0.56
Y_{GS} (mg)	-	x	-	-	1312	140	84.4	81.3	0.32
Y_{DM} (g)[1]	-	-	-	x	231	212	31.0	46.6	0.62

1. At 3, 6 and 9 weeks of regrowth.

Section 2.3.1). In the first 1977 crop of the monoculture (the cleaning cut and the top-dressings with 100 kg of nitrogen were carried out on 4 April 1977) and in the second 1975 crop of the mixed culture each plant was cut when 10 flowering heads had fully emerged (IHE). The fresh weight and Y_{DM} were determined.

Observations made in corresponding crops of the two cultures were compared. Spearman's rank-correlation coefficients, corrected for tied observations, were calculated between the means of the plants of the replicates of the two cultures, averaged over seasons if the characteristic had been observed in more than one season. The coefficients of variation were calculated from these means for each characteristic per culture.

4.3 RESULTS

In Table 26 the means and the coefficients of variation of most of the observed characteristics are presented together with the rank-correlation coefficients between the monoculture and mixed culture. It is evident that the competitive stress exerted by the Rhodes grass delayed the time of head emergence and depressed herbage and seed productivity in the population of 121 plants. The decrease in productivity was largely caused by the much lower number of tillers of the plants in the mixed culture than in the monoculture: tiller number and head number were halved.

The lower number of flowering heads resulted in a much lower Y_{CL} in the mixture. Germination figures of the seed harvested in the two populations were approximately equal (data not presented). In the individual plants of the mixture the Y_{GS} was depressed relative to that in the monoculture to the same extent as Y_{CL}. Y_{DM} did not decrease as much as would have been expected from the lower tiller number. However, by that time the setaria plants were all well established, while the competitive influence of the Rhodes grass was reduced because of its lack of persistence. The plants in the mixture adopted a more prostrate habit than the monoculture plants as expressed by the tiller angle. This was largely

because of the small circumference at the base of the plant due to the small number of tillers in the mixture. This smaller circumference, evident in the denominator of the tiller-angle ratio, thus had a positive effect on its size.

Towards 1976 sixteen genotypes of setaria had died in the mixed culture, one of them in all three replicates and one plant in two replicates, while the remaining plants had disappeared in one of the three replicates. This was caused by the poor growth vigour of these plants, for which reason they had been late in head emergence during the previous years. Y_{DM} of these missing plants were set at zero. No plants died in the monoculture.

Except for Y_{GS} all characteristics in the mixture showed a higher coefficient of variation than those in the monoculture, indicating that competitive stress widened the variation in the population.

The rank-correlation coefficients (Table 26) were fairly low for most characteristics, while tiller angle and Y_{GS} had very low rank-correlation coefficients. These two characteristics thus showed a higher degree of disorder in the relative ranking of the individuals - in Chapters 2 and 3, tiller angle and Y_{GS} were found to vary considerably from replicate to replicate and from season to season.

As regards the relationship between time of head emergence and Y_{DM} at IHE the behaviour of the two populations differed for the two cultures. In the mixed culture the simple correlation coefficient between these two characteristics was -0.663 ($P < 0.01$), which meant that early-heading plants had a higher Y_{DM} at IHE than late-heading plants. In the monoculture this correlation was 0.174. Though not significant, the correlation suggested that late-heading plants had a higher Y_{DM} at IHE than early-heading plants. The absolute Y_{DM} were not compared because of their different times of recording.

4.4 DISCUSSION

The relative ranking of the 121 genotypes as spaced plants in the monoculture and in a sward of Rhodes grass showed fairly poor agreement as regards the characteristics observed. Herbage and seed yield were suppressed in the mixed culture and the variation observed in the population was greater in the mixture than in the monoculture (Table 26).

A simple way to assess the variability within a population and to group the plants according to observed characteristics is to test at wide spacing in monoculture. When selection is carried out under these conditions, it has to be realized, in view of the results obtained in this study, that the selected plants will not be the same as those selected under more competitive stress.

It was found that the coefficients of variation for the measured characteristics, except Y_{GS}, were larger in the mixed culture than in the monoculture (Table 26). Spitters (1979) studying the effects of inter-genotypic competition and density of stand on the response to selection in barley, reported that inter-genotypic competition decreased as the result of wide spacing, which led to a lower coefficient of variation for the characteristic under study. The higher coefficient of variation in the mixed culture of setaria and Rhodes grass can thus be explained by the larger (inter-generic) competition occurring in this population than in the monoculture. Under wide spacing the competition between plants is eliminated, but this effect is replaced by a possibly different response of the geno-

types to the wide spacing (Spitters, 1979), which is corroborated by the results discussed in Section 2.4.3.

The size of the rank-correlation coefficients however suggests that selection at wide spacing might be applied at the initial stages of a breeding programme when differences between plants can still be easily distinguished. When the population has been narrowed after this first screening, a second, more laborious testing of the selected plants under more competitive stress in monoculture or mixed culture can then be carried out. Plants that performed well under wide spacing, but were poor under more intensive competition can be rejected. If seed of the finally selected plants becomes available, further testing and selection can be done in small swards in which individual setaria plants can still be recognised.

In temperate grasses, evaluation under spaced-plant conditions is often hampered by the occurrence of virus diseases as for instance in perennial ryegrass. Thanks to wide spacing, affected plants can be marked. Under sward conditions virus diseases are not so recognisable and diseased plants could disappear without being noticed, which is a clear disadvantage of plant evaluation at close density. In setaria, virus diseases have not yet been a problem and the spaced-plant population of 4000 plants of Nandi I (see Chapter 1) was maintained without virus problems for 7 years.

The leaf percentage of the plants in the mixture differed from and had accumulated more dead material than the plants in the monoculture (Table 27). The plants in the mixed culture were leavier than those in the monoculture because of slower growth, as expressed by the later time of head emergence of the former. In whole-plant comparisons, D_{vitro} would have been affected by this. In Section 2.4 it was stated that the observed range of D_{vitro} under sward conditions was much lower than under wide spacing, which was due in fact, as can be concluded from the present study, to their being different in morphological composition. In Section 2.4.3 the effects of spacing on D_{vitro} were further discussed.

The effect of Rhodes grass on the setaria plants was clearly expressed by the contrasting relationship in the two cultures as regards time of head emergence and Y_{DM} at IHE. In the mixture the competitive stress exerted by the Rhodes grass was maintained throughout the plant harvesting period whereas, in the monoculture, inter-plant competition changed with the removal of plants that had reached the stage of having ten fully emerged heads. Later-harvested plants had then, in addition to the already much longer time that they were allowed to grow, a further advantage over plants sampled earlier.

Table 27. Leaf percentage and percentage dead material at 3 periods of regrowth of 50 randomly chosen plants.

Weeks of regrowth	Culture	Leaf percentage	Percentage dead material
3	Mono	45.1	-
	Mixed	54.3	-
6	Mono	40.7	3.0
	Mixed	43.1	6.7
9	Mono	25.5	3.9
	Mixed	27.9	6.4

5 Productivity of plants with contrasting growth habit

5.1 INTRODUCTION

Within the spaced-plant population of 4000 plants of Nandi I (see Chapter 1) there was ample variability in growth habit (Boonman & Van Wijk, 1973). A close relationship was found between growth habit and time of head emergence : early-heading plants were tall and erect, while late-heading plants were short and prostrate. The individuals in so heterogeneous a population, when planted in a sward and subjected to repeated defoliation, can be expected to influence each other in growth.

Competition occurs when two or more organisms seek a common growth factor whose supply falls below the combined demand (Donald, 1963). The factors for which competition may occur are water, nutrients, light, space, oxygen and carbon dioxide. Donald (1963) assumed that most relationships between plants are competitive: when two fodder species are grown together they will not bring advantage in terms of dry matter over the higher-yielding species in monoculture - one is the agressor and the other is suppressed.

In Donald's concept there is no room for positive effects which plants may have on each other. According to De Wit (1960) there is competition when one component of the mixture gains at the expense of the other, but these gains and losses can be compensatory or complementary. If the gains and losses counterbalance, compensation results. If there is no counterbalance, complementation occurs which, in the positive direction, produces a mixture whose performance exceeds the average of its constituent monocultures and, in the negative direction, results in mixtures whose performance falls below their average monoculture. Intermediate forms of complementation can be distinguished.

Rhodes (1968, 1969) reported positive complementation between two contrasting varieties of perennial ryegrass. The yield of a mixture, consisting of an erect, long-leaved variety and a prostrate, short-leaved one was, with frequent cutting and high fertilizer input, significantly higher than the yields of these varieties grown in monoculture under the same management. Positive complementation also occurred on a single-plant basis with perennial ryegrass in an infrequent cutting system (Rhodes, 1970): a mixture of erect and lax-growing genotypes was more productive than its highest-yielding component in monoculture.

Negative complementation in mixtures occurs when the least productive component dominates the other, higher-yielding component(s) in monoculture. Montgomery (1912) found in cereals that the lowest-yielding variety in monoculture was able to survive in a mixture with a higher-yielding variety that was in monoculture at the expense of the latter. Consequently the yield of the mixture was below that of the best-yielding variety in monoculture. Because of this effect (subsequently called the Montgomery effect) and his own

experimental results, Van den Bergh (1968) advocated the use of monocultures in grasses.

Though possibly lower in dry-matter yield, mixtures of grasses have a clear advantage over monocultures in terms of yield reliability. Present grassland management requires not only a high dry-matter yield. An even distribution of the dry matter produced during the growing season which can be maintained over a number of years, is at least as important, if not more so than the total dry-matter yield. This can be achieved by the use of mixtures composed of different species or varieties, supplementing each other when one component of the mixture has suffered from stress conditions, such as disease attacks, adverse weather conditions or severe wearing. In a mixture of perennial ryegrass and timothy the latter may be more dominant after a severe winter, because of its better winter hardiness. Mixtures of timothy and meadow fescue, especially suited to continental conditions, are often supplemented with smooth-stalked meadow grass as a ground cover because of the creeping habit of the last named. In a mixture of Rhodes grass and setaria, the former can provide a fast and dense ground cover for the latter, which establishes itself more slowly and is more prone to weed invasion because of its tufted habit. Once established, setaria is more persistent than Rhodes grass. Early spring growth under temperate conditions is achieved by blending early and late-heading varieties.

Selection for earliness was found to be a tool for improving D_{vitro} and Y_{CL} (Chapters 2 and 3). Early-heading plants also had a higher fresh weight at seed harvest than late-heading plants (Table 8). Early-heading plants, however, were characterized by an erect growth habit (Table 8), which might affect the regrowth and persistence of such plants when subjected to repeated defoliation. An experiment was therefore set up to compare dry-matter production and persistance of these erect-growing plants with plants of a lax and prostrate growth habit at two cutting frequencies, grown in monoculture and in the four possible mixtures, the results of which are described here.

5.2 MATERIAL AND METHODS

During March 1973, root splits were collected from selected plants in the spaced-plant population of Nandi I. The plants were selected for an erect (E), lax (L) or prostrate (P) growth habit as observed in the 1970, 1971 and 1972 crops. Each growth habit was represented by thirty-six genotypes.

The root splits were multiplied vegetatively in a shaded nursery and on 28 May 1973 microswards were prepared in the field by planting the clones at a density of 25 plants per square meter. Each growth habit was grown in monoculture (36 genotypes) (E, L, P) and in mixtures of two (EL, EP and LP) and three (ELP) growth habits, which were of 72 and 108 genotypes, respectively. Plot sizes varied accordingly.

The swards were laid out in a split-plot design and incorporated two replicates. Two cutting frequencies (frequent and infrequent) were allocated to the main plots, while the 7 monocultures and mixed cultures were allocated to the subplots. Within each plot the genotypes were randomized and guard rows of corresponding plant types were planted around each plot. At time of planting 40 kg of phosphate per hectare was applied. On 19 June 1973, dead plants were replaced by spare plants from the nursery. All plants were cut back on 10 August 1973 to a height of 5 cm and the trial was top-dressed at a rate of 50 kg of nitro-

gen per hectare. No observations were made in the first year of planting.

On 21 March 1974 all plants were cut back. The main plots, marked out for frequent cutting (every three weeks) received 25 kg of nitrogen per hectare, while 50 kg of nitrogen per hectare was applied to the plots that were to be cut at six week intervals (infrequent cutting).

On 19 April 1974, the plots with the frequent cutting system were cut by hand at a height of 5 cm and the fresh weight per plot was determined. A sample of 500 g of fresh material was dried and its dry-matter content determined. Three weeks later the dry-matter yield of all plots was determined. Throughout the year, five cuts were made according to the infrequent system and ten cuts under the frequent system. After each cut the frequently cut swards were top-dressed with 25 kg of nitrogen per hectare and the infrequently cut swards received 50 kg per hectare.

In 1975 a cleaning cut was made on 21 March, after which the frequently cut plots were top-dressed at a rate of 25 kg of nitrogen per hectare and the other plots received nitrogen at a rate of 50 kg nitrogen per hectare. On 5 June 1975 the first cut of the 'frequent' plots was made. These plots were cut six times at monthly intervals in 1975, while the infrequent cutting was done at two-month intervals. The period of regrowth was extended compared to 1974 because of the slower growth rate. No yield data were recorded.

In the subsequent year, 1976, the cleaning cut was carried out on 13 April, followed by a nitrogen top-dressing similar to those of the previous years. In the first cut of 1976, on 27 May, each plant of the frequently cut plots was harvested individually and bulked per growth habit per mixture. Fresh weight and dry-matter content were determined. The monocultures were harvested in bulk. The same applied to the 'infrequent' plots on 30 June. In all, the frequently cut plots were cut four times during 1976, while the infrequently cut plots were harvested twice.

During January 1975 and January 1977 the number and types of plants that had died in each culture were assessed. The individual plants could still be distinguished.

In order to compare the yields of the monocultures and mixed cultures the yields of the monocultures and the binary cultures were converted to the size of the plot of the trinary culture, that is 4.32 m^2. An analysis of variance was carried out on the yield data for 1974. Means were compared using Duncan's new multiple-range test (Steel & Torrie, 1960).

The environmental variance among plants within plots of different sizes rises with increasing plot area. Consequently the environmental variance of the monocultures and the mixed cultures varied. Smith (1938) established a relationship between inter-plant variance and plot-size, according to which the environmental variance can be adjusted. However, this correction could not be applied as no yield data were taken on the individual plants.

5.3 RESULTS

The relative yields of the various cultures subjected to frequent and infrequent cutting and to both cutting frequencies are presented in Table 28, together with the percentage increase for infrequent cutting compared to frequent cutting. Significant differences in dry-matter yield between the yield totals of the cultures were established ($P < 0.05$). The

Table 28. Relative Y_{DM} and percentage increase of Y_{DM} at infrequent cutting compared to frequent cutting in 1974. Relative yields followed by the same letter do not differ significantly at $P < 0.05$.

Culture	Frequent cutting	Infrequent cutting	Total	Percentage increase at infrequent cutting
E	132	109 a	118 a	40
L	108 a	107 a	108 a b	68
P	103 a	98 a	100 a b c	61
EL	95 a	100 a	98 a b c	79
EP	93 a	91 a	92 b c	65
LP	75 a	92 a	86 c	109
ELP	93 a	103 a	99 a b c	87
Mean	100 = 1.35 kg/m^2	100 = 2.29 kg/m^2	100 = 1.82 kg/m^2	

difference between the two cutting frequencies was significant ($P < 0.01$), while no significant culture × cutting frequency interaction occurred. No particular growth habit was thus favoured by a particular cutting frequency.

The different cultures showed a wider range in dry-matter yield on frequent cutting than when cut infrequently (Table 28). At both cutting frequencies E was the highest-yielding culture. With the frequent system, E differed significantly from the other cultures, while with the infrequent cutting system there were no significant differences between the cultures to be observed. When both cutting frequencies were combined, E was in the similar non-significant range as L, P, EL and ELP were.

None of the mixtures outyielded their highest-yielding constituents in monoculture (Table 28). With frequent cutting the LP mixture was the lowest in yield. With infrequent cutting the differences between the mixed cultures were less pronounced than when cut frequently. Both cutting frequencies combined showed that EL and ELP were the highest-yielding mixtures, whereas LP lagged behind.

Of the various cultures, E showed the least increase (40%) in dry-matter yield on infrequent compared to frequent cutting (Table 28). This growth habit was thus the least affected by the frequency of cutting. The highest increase was displayed by the LP mixture (108%) and thus clearly responded to the longer regrowth period provided by the infrequent-cutting system.

Table 29. Expected and observed Y_{DM} of mixtures in 1974 (kg/m^2).

Culture	Frequent cutting			Infrequent cutting		
	Expected Y_{DM}	Observed Y_{DM}	Difference between observed and expected (%)	Expected Y_{DM}	Observed Y_{DM}	Difference between observed and expected (%)
EL	1.62	1.28	-21.0	2.48	2.29	- 7.7
EP	1.59	1.26	-20.8	2.37	2.08	-12.2
LP	1.42	1.01	-28.9	2.35	2.11	-10.2
ELP	1.54	1.26	-18.2	2.40	2.36	- 1.7
Total	6.17	4.81	-22.0	9.60	8.84	- 7.9

Table 30. Expected and observed yields of the components of the mixtures in the 1st cut of 1976 (g/m^2).

Culture	Component	Frequent cutting				Infrequent cutting			
		Expected	Observed	Difference between observed and expected (%)	Contribution of each component in the mixture (%)	Expected	Observed	Difference between observed and expected (%)	Contribution of each component in the mixture (%)
EL	E	155	152	- 1.9	56.1	240	200	-16.7	51.5
	L	131	119	- 9.2	43.9	217	188	-13.4	48.5
EP	E	155	151	- 2.6	55.3	240	198	-17.5	57.9
	P	153	122	-20.3	44.7	232	144	-37.9	42.1
LP	L	131	113	-13.7	46.7	217	170	-21.7	55.6
	P	153	129	-15.7	53.3	232	136	-41.4	44.4
ELP	E	155	128	-17.4	36.8	240	151	-37.1	32.0
	L	131	112	-14.5	32.2	217	188	-13.4	39.8
	P	153	108	-29.4	31.0	232	133	-42.7	28.2
Total		1317	1134	-13.9		2067	1508	-27.0	

From the respective dry-matter yields of the monocultures obtained with the two cutting frequencies, the expected yields of the mixtures were calculated by summing the yields of their constituents in monoculture, the results of which are given in Table 29. It was assumed that the plants of different growth habits still occurred in the same frequency as planted. The expected values were higher than the observed values, which meant that the various growth habits affected each other in the mixture negatively, resulting in mixtures whose performance fell below their monoculture average. In the frequent-cutting system the mutual depression of the components of the mixtures was greater than when infrequently cut. At longer periods of regrowth the plants did not inhibit each other so strongly in growth as when frequently cut.

On frequent cutting, the LP mixture showed the highest suppression; the other mixtures were suppressed approximately to the same extent. With infrequent cutting, the ELP mixture almost achieved compensation as the expected and the observed yields were approximately equal.

The contribution of each growth habit to the yield of the mixture was assessed in the first cut of 1976. The yield of each growth habit in a mixture was compared with that of the corresponding monoculture as recorded at the same cut. The results are given in Table 30. In contrast with the results obtained in 1974 (Table 29), the yields for infrequent cutting were suppressed more than those for frequent cutting. In the binary mixtures, plants of the erect growth habit were almost unaffected by mutual competition in the frequent-cutting system, which is expressed by the slight differences between the expected and the observed yields. The prostrate growth habit was suppressed most in dry-matter production by mutual inhibition, especially with the infrequent-cutting system. The erect and lax growth habit did not differ to a large extent in the binary mixtures, but in the trinary mixture the erect growth habit displayed greater depression than the lax growth habit.

The proportions of the individual contributions of the constituents to the yields

Table 31. Percentage dead plants of each growth habit in the monocultures and in the mixed cultures in January 1974 and 1977.

Growth habit	Frequent cutting		Infrequent cutting	
	1974	1977	1974	1977
Monocultures				
E	0	11.1	6.9	11.1
L	8.3	9.7	11.1	12.5
P	6.9	19.4	8.3	29.2
Total	5.1	13.4	8.8	17.6
Mixed cultures				
E	4.2	3.7	6.0	12.0
L	6.5	11.6	7.9	13.4
P	5.6	15.3	17.1	28.7
Total	5.4	10.2	10.3	18.0
Overall total	5.3	11.0	10.0	17.9

of the mixtures did not differ markedly from the proportions in which the mixtures were originally planted (Columns 6 and 10 of Table 30).

More plants had died in the course of application of the infrequent-cutting system than with the frequent-cutting system after the 1974 season and in 1977 (Table 31). This caused greater suppression in dry-matter yield of the components in the mixtures under the infrequent-cutting system compared to the frequent-cutting system as determined in the first cut of 1976 (Table 30). The prostrate growth habit showed the lowest survival rate in 1977, while that of the erect and lax growth habit was roughly similar. Most dead plants occurred in the LP mixture (data not presented).

5.4 DISCUSSION

In grasses, tillers produce new leaves after defoliation at the expense of the reserve substances stored in the stubble and the plant roots. During this regrowth period the assimilates of the new-formed leaves will contribute to further increase in leaf surface.

If there are no differences in photosynthetic activity between species, varieties or individual plants under sward conditions, yield differences will be largely determined by the length of the regrowth period during which growth will be exponential. This growth rate is determined by the amount of the residual leaf area left after defoliation, which in turn is influenced by the growth habit of the grass, cutting frequency and cutting height.

Species that spread by means of rhizomes or stolons have a larger leaf area left after defoliation than tussock-forming species. In this latter group a distinction can be made between erect and prostrate-growing plants, the latter having a larger residual leaf area after cutting.

A higher cutting frequency will result in more regrowth periods and will cause a drop in yield especially in erect, tussock-forming species due to constant demand on the reserve substances which will ultimately result in weakening of the plant.

Cutting height will influence the amount of photosynthetically active material left. Especially in tropical grasses with their continuous stem elongation, height of cutting determines the number of growing points left. If ample reserve substances are present, buds in the lower tillers can grown again, but this takes longer than when the growing points are left undisturbed.

Comparison between the setaria plants with different growth habits revealed the erect monoculture as the most productive with both the frequent and infrequent cutting systems (Table 28). The erect growth habit also proved to be the strongest competitor at both cutting frequencies and cutting height applied (Table 30), resulting in the highest survival rate (Table 31).

The results obtained in the present study were not in agreement with the processes described above, from which the prostrate growth habit was expected to be a strong competitor and to have great persistence.

Boonman & Van Wijk (1973) reported a strong correlation between growth habit, growth vigour and time of head emergence. Similar relationships were observed within the population of 108 genotypes used in this experiment. The average time of head emergence of the

erect, lax and prostrate growth habits, as scored in the spaced-plant population of Nandi I in four consecutive crops of 1970, 1971 and 1972 (data not presented) was 2.7, 3.6 and 5.2 weeks, respectively. Growth vigour, scored on a 1-5 scale, with 5 representing the greatest vigour, in the similar crops, was 3.5, 2.9 and 2.6 for the erect, lax and prostrate growth habits, respectively. The prostrate growth habit was thus characterized by a later time of head emergence and a poorer growth vigour than the others. The low dry-matter yield of the prostrate growth habit at these particular cutting frequencies and heights must therefore mainly be attributed to the poor growth vigour of these plants, thus offsetting the advantage that this type of plant may have from its larger residual area after defoliation. The lax growth habit can be considered as intermediate between the erect and prostrate growth habits.

Rhodes (1971) attributed the interaction between varieties with a contrasting growth habit and cutting frequency as observed in perennial ryegrass to the fact that erect-growing varieties could utilize incident light more efficiently, which favoured this variety type when cutting was infrequent, whereas frequent cutting benefitted the prostrate growing variety because of the larger residual leaf area. Such an interaction was not significant in the setaria experiment and it is therefore concluded that at the cutting height concerned the cutting frequency did not result in a change in response of the various growth habits to cutting frequency.

In terms of dry-matter yield the erect growth habit emerged as the strongest competitor under the frequent-cutting system at the cutting height applied, while the prostrate growth habit was the poorest. Under the infrequent-cutting system the erect and lax growth habits had approximately the same competitive ability, while the prostrate growth habit was evidently poorer. Furthermore, the erect growth habit showed the lowest percentage of dead plants.

These results agree with those of Hill & Shimamoto (1973) and to a certain extent with those obtained by Hacker (1978 and pers. comm.). Hill & Shimamoto (1973) reported that a genotype of perennial ryegrass with long leaves and an erect growth habit was the strongest competitor of five genotypes with different growth habits in terms of dry-matter yield at two cutting frequencies. However, in Hill & Shimamoto's experiment the strongest competitor was not the highest-yielding component. Hacker (1978) recorded the flowering characteristics of survival populations of six Nandi setaria pastures, grazed for six years at different stocking rates (2.5, 4.3, 6.2 and 8.0 animals per hectare) and at two fertilizer inputs (280 and 476 kg of nitrogen per hectare). For both high and low nitrogen treatments the populations derived from the more heavily stocked paddocks flowered consistently earlier than those from paddocks more lightly stocked. Ratings for growth habit indicated that the populations did not differ. As already shown in this section, earliness was clearly connected with erectness, and the results of Hacker's study could well corroborate the findings of this experiment that the erect growth habit had the greatest competitive ability.

The higher death rate of the prostrate plants in the monocultures and the mixtures is evident from Table 31. Though not completely comparable because of the different years of observation, the low survival rate of this growth habit did not reduce its relative contribution to the final yield of the mixtures to a great extent (Table 30). Compared

to the other growth habits, the contribution of the prostrate growth habit was based on a small number of plants with a high individual dry-matter yield.

According to Donald (1968), strong competitive ability of plants in monocultures of cereals will lead to heavy mutual depression among the crowded plants. Donald (1968) therefore suggested the creation of varieties consisting of plants resistant to crowding, each plant making efficient use of its limited environment. Within the monoculture of the prostrate plants, intra-type competition was the strongest because of its prostrate growth habit and consequently its large circumference. The prostrate growth habit therefore was the most susceptible to mutual crowding.

In the present study only overground competition was measured by yield determinations and survival rates and no mention was made of the underground competition, but as no observations were made on this, underground competition could not be quantified. In general it can be said that the root mass of grasses cut frequently is smaller than that of grasses cut infrequently.

6 Simultaneous selection for herbage and seed yield

6.1 INTRODUCTION

Grass breeders in Western Europe have mostly relied on selection within populations of indigenous species collected from traditionally productive grasslands in which natural selection had played its part, depending on the type of management imposed. Unlike arable cash crops, breeding objectives of grasses were broadly defined as aiming at the development of varieties with improved dry-matter yield, leafiness and persistence. This and similar sources from which the initial breeding material was collected have led to a multiplicity of varieties, differing only in minor characteristics within the various maturity groups.

In the late sixties, breeders from all Dutch grass-breeding firms collected material of perennial ryegrass in the south-east of the Netherlands (Lackamp, 1977). This material was compared in government institutes with the then existing varieties. It was found that the varieties were superior to the indigenous material in disease resistance and seed productivity, but that the herbage yield of the varieties was hardly any better than that of the wild material. Thus, in spite of all breeding efforts, large increases in dry-matter yield had not been achieved.

Differences in herbage productivity between varieties are largely determined by the length of the regrowth period if there are no differences in photosynthetic activity between individual plants under sward conditions as outlined in Section 5.4. This, and the fact that selection was usually made under spaced-plant conditions, which are different from the sward conditions under which the variety will be ultimately used (Chapter 4), have been the cause of the low selection response in dry-matter yield.

In the last two decades more intensive grassland systems have been developed, with higher nitrogen inputs and stocking rates, which demanded grass varieties that could meet these requirements. Moreover, in order to ensure the breeders protection for a new variety, it must be clearly distinct from already existing ones, and it must at least have reached the same level of uniformity as existing varieties, while during its multiplication the variety has to have proved its stability. To suit the higher management stress on the varieties and to fulfil the requirements of distinctness, uniformity and stability, breeding objectives have to be clearly established nowadays.

In addition to the more refined definition of the breeding objectives, which has led and will lead to clearly distinguishable varieties, chromosome manipulation (the development of tetraploid ryegrasses) and genera and species crossings (the development of *Festulolium* hybrids and the hybrids between the *Lolium* species) have further increased or will increase the varietal scope.

In developing the varieties described above, mass selection, which is selection based on the individual phenotype, has been and is being widely applied. The success of mass

selection depends on how accurately plants with a superior breeding value, based on the additive gene effects, can be recognized from their phenotypic expression, which is made difficult by the presence of non-additive genetic effects (i.e. dominance and epistasis) and enivronmental effects. Non-additive genetic variance comes to the front especially in food crops, such as cereals and maize, which have undergone cultivation and selection for thousands of years. Grasses, with their relatively short history as an intensively managed crop, display a high degree of additive variance, which accounts for the rapid responses achieved by mass selection for characters such as growth habit, persistence and resistance to diseases.

Contrary to the general view that highly evolved and developed plant populations lack additive variance, Gardner (1963) and Zuber et al. (1971) reported the occurrence of a considerable degree of additive genetic variance in open-pollinated varieties of maize. Around the year 1925 it was generally believed that American maize varieties could not be further improved by mass selection, though there was no critical evidence which supported this view (Sprague, 1966).

The ineffectiveness of mass selection was thought to be caused by overdominance (Hull, 1945; 1964). According to Hull (1945; 1964), continuous selection of superior plants, heterozygotes owing to the action of overdominance, had led to an equilibrium of gene frequencies, instead of to the accumulation of favourable dominant genes. The additive variance was thought to be exhausted. Gardner (1961) attributed the poor response of mass selection to environmental effects, including genotype × environment interactions, which hampered the recognition of plants with a high breeding value. Therefore Gardner (1961) applied so-called grid selection by which these effects were minimized: selection fields were stratified into small areas and seed of the highest-yielding 10% of the plants in each stratum were selected.

The alternative to mass selection is selection based on progeny means. Latter (1964) recommended progeny testing for characteristics with a low heritability. Breese & Hayward (1972), however, cautioned against the inclusion of progeny testing in the breeding scheme for grasses, as that would give too much importance to sexual reproduction when characteristics associated with asexual reproduction (vegetative growth and regrowth) have to be improved. Breese & Hayward (1972) argued that progeny testing might be useful in acquiring information on the performance of the plants under the competitive conditions of a sward, which is not the case with single plants at wide spacing. To bypass this problem, Van Dijk (1973) tested spaced plants and clonal rows in a dense sward of another species to imitate sward conditions as discussed in Chapter 4.

The advantages of mass selection as compared to other selection methods based on progeny tests are:

- the large number of plants that can be evaluated, so that the selection intensity can be high without any necessary increase in the rate of inbreeding;
- one cycle per generation;
- the relative simplicity of operation.

In view of the foregoing it seems fully justified to apply mass selection to grasses, especially tropical grasses, in which field virtually no breeding work has been done: most commercialized Kitale varieties were introductions out of the local flora. Some selection

may have occurred during the maintenance of the collected material in small plots because of the cutting and grazing imposed, but it can be assumed that the larger part of the variance present is additive in nature.

The efficiency of mass selection can be increased by the simultaneous selection of two or more characteristics, for which three methods are available: tandem selection, independent culling levels and index selection. In tandem selection one characteristic is selected at a time until that one has been improved, then a second is considered, etc. With independent culling levels a certain level of merit for each characteristic is set and individuals below that level are discarded regardless of the superiority or inferiority of the others. In index selection each individual is given a score combining several characteristics, weighted according to their relative importance. Hazel & Lush (1942), Young (1961), Young & Weiler (1961), Elgin et al. (1970) and Eagles & Frey (1974) compared these three methods and found that index selection was the most efficient in improving the net worth of the selection.

The aim of selection is to select plants with a superior breeding value, that is plants that give the highest response to the defined breeding objectives. If there are m characteristics (Y-characteristics) of economic importance to be considered in the breeding objective, the total worth of a plant is expressed by its aggregate breeding value H, also called aggregate genotype. The aggregate breeding value is defined as the sum of m breeding values (assuming a distinct breeding value for each characteristic), each breeding value weighted according to the relative economic importance of that characteristic (Hazel, 1943):

$$H = v_1G_1 + v_2G_2 + \ldots\ldots\ldots\ldots v_mG_m = \sum_{j=1}^{m} v_jG_j,$$

in which

H = the aggregate breeding value
v_j = the relative economic importance of the j^{th} characteristic
G_j = the breeding value or additive genetic value of the plant for the j^{th} characteristic

As the breeding value of a plant is not measurable owing to the presence of non-additive and environmental effects, the estimation of the aggregate breeding value has to be based on the phenotypic expression of the plant through a selection index I. I is a linear function of n phenotypic observable characteristics (X-variates), with each one weighted as follows:

$$I = b_1P_1 + b_2P_2 + \ldots\ldots\ldots\ldots b_nP_n = \sum_{i=1}^{n} b_iP_i,$$

in which

I = selection index
b_i = the weighting factor of the i^{th} characteristic
P_i = the phenotypic observation of the i^{th} characteristic of the plant.

Characteristics occurring in H (the aggregate breeding value) and I (the index) are not necessarily the same.

The purpose of the selection index is to select plants with the highest rank for H from the information supplied by the characteristics present in I, in which each is given a weight b_i. The weighting factors b are determined by maximizing the correlation between H and I (Smith, 1936; Hazel, 1943). The appropriate b-values are solutions to the following n equations:

$$
\begin{aligned}
b_1P_{11} + b_2P_{12} + \cdots\cdots b_nP_{1n} &= v_1G_{11} + v_2G_{12} + \cdots\cdots v_mG_{1m} \\
b_1P_{12} + b_2P_{22} + \cdots\cdots b_nP_{2n} &= v_1G_{21} + v_2G_{22} + \cdots\cdots v_mG_{2m} \\
\cdots\quad & \cdots\quad \cdots\quad \cdots\quad \cdots\quad \cdots\quad \\
\cdots\quad & \cdots\quad \cdots\quad \cdots\quad \cdots\quad \cdots\quad \\
\cdots\quad & \cdots\quad \cdots\quad \cdots\quad \cdots\quad \cdots\quad \\
b_1P_{1n} + b_2P_{2n} + \cdots\cdots b_nP_{nn} &= v_1G_{n1} + v_2G_{n2} + \cdots\cdots v_mG_{nm}
\end{aligned}
$$

in which

P_{ii} = the phenotypic variance of the i^{th} characteristic of I
P_{ik} = the phenotypic covariance between the i^{th} and the k^{th} characteristic of I
G_{ij} = the genotypic covariance between the i^{th} characteristic of I and the j^{th} characteristic of H
b_i = the weighting factor of the i^{th} characteristic of I
v_j = the relative economic value of the j^{th} characteristic of H

Therefore the information needed to solve these equations is:
- the phenotypic variances and covariances of the characteristics of I;
- the genotypic covariances between the characteristics of I and H;
- the genotypic variances of the characteristics of H;
- the relative economic values of the characteristics of H.

The n equations can also be represented by the matrix notation

$$P\,b = G\,v \qquad (1)$$

in which

P = an n x n phenotypic covariance matrix between the characteristics of I
b = a column vector of n weighting factors
G = an n x m genotypic covariance matrix between the characteristics of I and H
v = a column vector of m relative economic weights of the characteristics of H.

The weighting factors b are solved from

$$b = P^{-1}G\,v \qquad (2)$$

When solving the weighting factors, σ_I^2 is set equal to σ_{IH}, which means that the regression of I on H is unity and that their correlation is $r_{IH} = \sigma_I/\sigma_H$.
The variance of the index, the variance of the aggregate breeding value and the covariance between the index and aggregate breeding value are respectively:

$$\sigma_I^2 = b' P b \tag{3}$$

$$\sigma_H^2 = v' C v \tag{4}$$

$$\sigma_{IH} = b' G v = b' P b \tag{5}$$

in which

C = an m x m genotypic covariance matrix between the characteristics of H
b' = the transpose of b
v' = the transpose of v

The response to selection of the aggregate breeding value is

$$G = k.r_{(I,H)}.\sigma_H \tag{6}$$

in which

G = response to selection
k = standardized selection differential, which is called the selection intensity
$r_{(I,H)}$ = correlation coefficient between the index I and the aggregate breeding value H
σ_H = standard deviation of the aggregate breeding value H

As $r_{(I,H)} = \sigma_I/\sigma_H$, because σ_I^2 was set equal to σ_{IH} when solving the weighting factors b, it follows that $G = k.\sigma_I$. The response to selection is therefore equal to the product of the selection intensity and the standard deviation of the index and is expressed in economic units.

Formula (6) can also be written as

$$G = k.\frac{\sigma_{IH}}{\sigma_I} \tag{7}$$

Multiplying the numerator and the denominator of formula (7) with σ_I gives

$$G = k.\sigma_I.\frac{\sigma_{IH}}{\sigma_I^2} = k.\sigma_I.\, b_{(H,I)} \tag{8}$$

where $b_{(H,I)}$ is the regression coefficient of H on I.

From equation (8) it thus follows that the response to selection, expressed in the units of measurement, is the product of the selection intensity, that is the standard

deviation of the index and the regression of a characteristic of the aggregate breeding value H on index I.

Cunningham (1969) expressed the value of each variate in the index as

$$100 - \sqrt{\frac{b'Pb - \frac{b_i^2}{W_{ii}}}{b'Pb}} \times 100 \qquad (9)$$

in which W_{ii} = the i^{th} diagonal element of the inverse of P. This value represents the percent reduction in genetic gain for the aggregate breeding value if that variate were omitted from the index.

The phenotypic and genotypic variances and covariances required for the calculation of selection indices of cross-fertilizing crops can be estimated from sib-relationships after an offspring has been obtained or, if the crop can be propagated vegetatively, from clonal replication.

Selection indices can also be constructed from parent-offspring relationships without first determining the population parameters. As the best estimate of the breeding value of half-sibs is given by twice the mean deviation of the progeny from the population mean (Falconer, 1960), De Wolff (1972) suggested the construction of selection indices by equating the weighting factors b_i to twice the partial regression coefficients for the multiple regression of the weighted sum of the progeny means for the characteristics to be improved on the n observed variates of the parent population.

The selection index depends on the definition of the aggregate breeding value. Young (1961) showed that the efficiency of the index increased with a rise in the number of characteristics and decreased with increasing differences in their relative importance. Gjedrem (1972) concluded that all characteristics of economic importance had to be included in the aggregate genotype, leaving undecided how to determine those which are thought to be of economic importance. Usually those characteristics are chosen which are thought most practical to record.

The major drawbacks of index selection are:

- the difficulty in obtaining reliable estimates of phenotypic and genotypic variances and covariances and
- the problem of assigning them realistic economic values.

To avoid estimating the phenotypic and genotypic (co)variances, Brim et al. (1959) suggested the use of indices in which the characteristics and variates are weighted by their economic worth only. Such an index was called base index by Williams (1962). Base indices and indices estimated from phenotypic and genotypic (co)variances with assigned economic values to the Y-characteristics as developed by Smith (1936) and Hazel (1943) were found to be equally efficient (Elgin et al., 1970; Eagles & Frey, 1974 and Suwantaradon et al., 1975).

To avoid the assignment of economic weights, Pesek & Baker (1969; 1970) proposed the application of desired genetic gains, in which the amount of gain to be anticipated is defined. These values replace the relative economic weights of the characteristics in the

calculation of the index. This method can only be applied however when the P- and G-matrix have the same dimension, i.e. the characteristics of the index are similar to those of the aggregate breeding value, which is most unrealistic.

6.2 THE APPLICATION OF INDEX SELECTION TO THE SETARIA POPULATION OF 121 PLANTS AND THE OFFSPRING OF THAT POPULATION

As has been pointed out in Section 6.1, the characteristics occurring in H (the aggregate breeding value) and I (the index) do not need to be similar. In that case selection on the Y-characteristics is carried out through the X-variates and is thus an indirect selection of the Y-characteristics. This would be especially meaningful if the heritability of the Y-characteristics were low, while that of an X-variate correlated with the Y-characteristic had a higher heritability. The efficiency of index selection could be raised further if the indirect selection of the Y-characteristics through the X-variates could be carried out before flowering.

From Chapers 2 and 3 the variation present for herbage and seed yield in the spaced-plant population of the 121 setaria plants is evident. The positive correlation between the fresh weight of the plant at seed harvest and seed yield is given in Chapter 3, as a consequence of which selection for seed yield was expected not to affect herbage yield adversely. Boonman & Van Wijk (1973) found a positive correlation between growth vigour (as visually assessed one month after the cleaning cut) and seed yield in setaria and Rhodes grass.

To elaborate the relationship between herbage and seed yield, selection indices combining these 2 characteristics in an aggregate breeding value were calculated for the spaced-plant population and the open-pollinated offspring of this population. In Section 6.3 selection indices are constructed, based on genotypic and phenotypic (co)variances, estimated from clonal replication of the 121 plants, while in Section 6.5 selection indices are calculated from the parent-offspring relationship after analyzing the offspring dealt with in Section 6.4. The X-variates are those described in Appendix 1 and tested in Sections 2.2.1 and 3.3.1.

The 2 characteristics in the aggregate breeding value have thus to be weighted according to their economic value. Brim et al. (1959), selecting on oil and protein content in soybeans simultaneously, weighted the two characteristics according to their relative price ratio, based on a long-term average. Two other sets of economic values were included, representing extremes which had never been encountered. Eagles & Frey (1974) also used the relative market prices for oat grain and straw yields of oats in selection indices aimed at the simultaneous improvement of both characteristics. De Wolff (1972) constructed indices for the selection on resistance to lodging and yield in maize. The value of the former characteristic relative to the latter was estimated by assuming that the grain harvested from lodged plants had only half the value of grain harvested from erect plants. In selection indices with several agronomic characteristics in maize, two sets of arbritarily chosen economic weights were used (Suwantaradon et al., 1975).

It is evident that if two or more characteristics with a specific economic worth have to be improved, economic weights reflecting their respective market price can be assigned

directly. Agronomic characteristics, however, are more difficult to express in economic terms.

In the study here reported the aggregate breeding value comprised the breeding value for two characteristics: herbage yield and seed yield. Seed has a distinct commercial value and can therefore be assigned an economic worth, but the assignment of an economic weight to herbage yield is much more complicated, as herbage is only an intermediate product. The final, economic worth of herbage can only be assessed through the animal in the form of milk, meat or fibre produced.

It is, however, most speculative to express the economic worth of herbage per unit area through the animal's products and will only be applicable to the specific conditions under which the determinations were carried out. The figure found will be subject to the animal's breed, the management of the animal and the management of the ley.

In view of the unrealistic figures which result from the assignment of relative economic weights based on a cost analysis of herbage and seed production, the following three sets of relative economic weights were arbitrarily chosen for this study:

	A	B	C
herbage yield (Y_{DM} or Y_{DOM})	1	1	5
seed yield (Y_{CL} or Y_{GS})	5	1	1

Set C was included for methodological rather than agricultural reasons, as these economic values are unrealistic in agricultural terms. Set A reflected the importance of the availability of seed for the establishment of pastures. Set B represented an intermediate situation between A and C.

6.3 SELECTION INDICES CALCULATED FROM THE 11 X 11 TRIPLE LATTICE

6.3.1 Material and methods

Selection indices for the simultaneous selection on herbage and seed yield were calculated from the spaced-plant population of 121 plants of Nandi I, which has been described in Section 2.2.1.

The following 11 X-variates were included in the indices:

- tiller number;
- time of head emergence;
- tiller angle;
- tiller length;
- leaf number;
- leaf width;
- leaf length;
- stem diameter;

- tiller weight;
- fresh weight of the plant;
- head number.

A description of these characteristics is given in Appendix 1 and an account of their recording during the 1974 and 1975 crops has been given in Sections 2.2.1 and 3.3.1. The observed data were summed per entry and per replicate over the three crops.

Y_{DM} and Y_{DOM} were determined in 2 series of measurements in 1976 at three periods of regrowth as described in Section 2.3.1. The herbage yields were summed per entry and per replicate over both series. As replicates were confounded with time of regrowth, the yield of each plant was expressed relatively to the mean of the replicate in which it occurred.

Y_{CL} and Y_{GS} were summed per plant and per replicate over the three crops of 1974 and 1975 as mentioned in Section 3.3.1.

Two aggregate breeding values were composed: one consisting of the characteristics Y_{DM} and Y_{CL} and the other of the characteristics Y_{DOM} and Y_{GS}.

The model, as described in Section 2.2.1, was used for the analysis of variance. From this analysis, as presented in Table 5, the genotypic and phenotypic variances were estimated according to the equations presented in Section 2.2.1. For the analysis of covariance the same model and analysis similar to that in Table 5 were applied, but instead of the mean squares, the mean products between the various characteristics were calculated.

Selection indices for the two types of aggregate breeding values, each with the three sets of relative economic weights, were calculated according to Equation 1 as presented in Section 6.1.

After estimating vector b (see Eqn. 2), the standard deviation of the index, the standard deviation of the aggregate breeding value and the correlation between the index and the aggregate breeding value were calculated from Equation 3, 4 and 5 respectively, presented in Section 6.1.

The expected response to index selection for each characteristic in the aggregate breeding value was calculated according to Equation 8. These responses were expressed as percentages of their means.

As selection indices with n = 11 variates are cumbersome to apply, some discrimination was required to reduce the number of variates, with the aim of obtaining a subset of variates equally accurate in predicting the aggregate breeding value as the full set of variates. The value of each variate in the index was therefore calculated according to Equation 9. This value expresses the reduction percentage in rate of genetic gain of the aggregate breeding value if that variate were dropped from the index. The variate with the lowest value was omitted, after which the index was calculated anew on the basis of the remaining variates.

6.3.2 Results

The genotypic and phenotypic correlation coefficients between the X-variates and between the X-variates and Y_{CL} and Y_{GS} have been presented in Tables 8 and 23 and discussed in Chapters 2 and 3 together with the results of the analyses of variance. The correlation

coefficients between the X-variates and Y_{DM} and Y_{DOM} are shown in Table 32. The mutual correlation coefficients of the Y-characteristics were:

$Y_{DM} - Y_{CL}$ $\quad r_g = 0.731 \quad r_{ph} = 0.551$
$Y_{DOM} - Y_{GS}$ $\quad r_g = 0.659 \quad r_{ph} = 0.414$

The correlation coefficients between the Y-characteristics were high. Selection for one would therefore give a clear response of the other.

A pattern of correlations between the X-variates (without head number) and herbage yield (see Table 32) similar to that of the simple correlation coefficients between these characteristics at three, six and nine weeks of regrowth (Table 15) emerged from the genotypic and phenotypic correlation coefficients. The results have been discussed in Section 3.2.

In Table 33, selection indices in which the aggregate breeding value was composed out of Y_{DM} and Y_{CL} are given with the full number (i.e. n = 11) of X-variates, three sets of economic values included. Selection indices for the simultaneous selection on Y_{DOM} and Y_{GS} are shown in Table 34. Indices with subsets of X-variates for both cases are given in Appendix 3.

The correlation between the index and the two aggregate breeding values was high, thanks to the high genotypic correlations of some X-variates with the Y-characteristics. The correlation between the index and the aggregate breeding value was higher when herbage yield was given a greater economic weight in relation to seed yield.

Fresh weight of the plant and number of heads were the two most influential variates in the index, whose aggregate breeding value consisted of Y_{DM} and Y_{CL} (Table 33). When the least influential variates were eliminated step by step, head number remained at the economic values of Sets A and B and fresh plant weight for Set C. The correlations between the sub-index, consisting of the remaining variate and the aggregate breeding value, were 0.5047, 0.5149 and 0.6801, respectively. The correlation between the index and the breeding

Table 32. Genotypic and phenotypic correlation coefficients between X-variates and herbage yield.

	Y_{DM}		Y_{DOM}	
	r_g	r_{ph}	r_g	r_{ph}
Tiller number	0.668	0.552	0.668	0.544
Time of head emergence	-0.146	-0.204	-0.139	-0.190
Tiller angle	-0.056	-0.089	-0.056	-0.087
Tiller length	0.599	0.480	0.593	0.477
Leaf number	0.270	0.273	0.274	0.269
Leaf width	0.344	0.191	0.338	0.190
Leaf length	0.514	0.402	0.527	0.411
Stem diameter	0.301	0.173	0.345	0.130
Tiller weight	0.593	0.463	0.592	0.466
Fresh weight of the plant	0.968	0.617	0.918	0.713
Head number	0.582	0.504	0.579	0.498

Table 33. Selection indices for the simultaneous selection for Y_{DM} and Y_{CL}.

$v_{Y_{DM}}$ = assumed economic weight of Y_{DM}.

$v_{Y_{CL}}$ = assumed economic weight of Y_{CL}.

σ_I = standard deviation of I.

σ_H = standard deviation of H.

r_{IH} = correlation coefficient between I and H.

$G_{Y_{DM}}$ = expected response of Y_{DM} to index selection expressed as a percentage of the mean.

$G_{Y_{CL}}$ = expected response of Y_{CL} to index selection expressed as a percentage of the mean.

k = selection intensity

X-Variate	Index weights			Value of each variate (%)		
$v_{Y_{DM}} : v_{Y_{CL}}$	1:5 (A)	1:1 (B)	5:1 (C)	1:5 (A)	1:1 (B)	5:1 (C)
Tiller number	0.2300	0.1777	0.1966	0.8535	1.0277	1.2770
Time of head emergence	0.9651	0.7279	0.7819	0.2042	0.2340	0.2740
Tiller angle	0.5663	0.4661	0.5524	0.2492	0.3402	0.4850
Tiller length	0.3757	0.2717	0.2763	1.0523	1.1083	1.1631
Leaf number	-0.4145	-0.2428	-0.1681	2.6682	1.8351	0.8883
Leaf width	0.2155	0.1248	0.0839	0.7697	0.5187	0.2376
Leaf length	-0.1049	0.0714	0.2763	0.0133	0.0124	0.1891
Stem diameter	0.7581	0.5516	0.5658	0.3792	0.4043	0.4315
Tiller weight	0.7379	0.5041	0.4703	0.7257	0.6787	0.5988
Fresh weight of the plant	0.0770	0.0583	0.0630	2.2438	2.5964	3.0768
Head number	0.1302	0.0791	0.0596	4.0240	2.9729	1.7006
σ_I	39.8874	28.1079	27.9096			
σ_H	56.3919	37.2044	35.4156			
r_{IH}	0.7073	0.7555	0.7881			
$G_{Y_{DM}}$	20.2k	20.6k	20.9k			
$G_{Y_{CL}}$	31.5k	31.3k	30.6k			

value was not markedly affected by the elimination of tiller number, time of head emergence, tiller angle, tiller length, leaf number, leaf width, leaf length and stem diameter, but the elimination of tiller weight, fresh weight of the plant or head number did cause a substantial reduction in the correlation coefficient.

The variates tiller number and time of head emergence (Sets A and B) or fresh weight of the plant (Set C) exerted the greatest influence on the index whose aggregate breeding value comprised Y_{DOM} and Y_{GS} (Table 34). The stepwise elimination of the least influential variates resulted in an index comprising solely the variate fresh weight of the plant, which was similar for all three sets of economic weights. The correlations between this index and the aggregate genotype were 0.4655, 0.5258 and 0.6276 for the sets of economic weights A, B and C, respectively. The elimination of time of head emergence and tiller length in Sets A and B and the elimination of tiller number and tiller weight in Set C markedly decreased the correlation coefficient between the index and the aggregate breeding value.

Table 34. Selection indices for the simultaneous selection for Y_{DOM} and Y_{GS}.

$v_{Y_{DOM}}$ = assumed economic weight of Y_{DOM}.

$v_{Y_{GS}}$ = assumed economic weight of Y_{GS}.

σ_I = standard deviation of I.

σ_H = standard deviation of H.

r_{IH} = correlation coefficient between I and H.

$G_{Y_{DOM}}$ = expected response of Y_{DOM} to index selection expressed as a percentage of the mean.

$G_{Y_{GS}}$ = expected response of Y_{GS} to index selection expressed as a percentage of the mean.

k = selection intensity.

X-Variate	Index weights			Value of each variate (%)		
$v_{Y_{DOM}} : v_{Y_{GS}}$	1:5 (A)	1:1 (B)	5:1 (C)	1:5 (A)	1:1 (B)	5:1 (C)
Tiller number	0.8583	0.4929	0.3247	5.1056	4.3263	2.7924
Time of head emergence	7.0248	3.7741	2.0330	4.6513	3.4417	1.4823
Tiller angle	-0.2980	0.0226	0.3523	0.0290	0.0004	0.1566
Tiller length	1.0047	0.5821	0.3924	3.1961	2.7613	1.8720
Leaf number	-0.6829	-0.3741	-0.2149	3.0491	2.3516	1.1563
Leaf width	0.3141	0.1702	0.0943	0.6868	0.5195	0.2387
Leaf length	-1.5082	-0.6112	0.0413	1.1645	0.4917	0.0034
Stem diameter	1.2519	0.8257	0.7299	0.4347	0.4879	0.5717
Tiller weight	1.0574	0.6570	0.5194	0.6230	0.6204	0.5811
Fresh weight of the plant	0.1433	0.0902	0.0733	3.2783	3.3546	3.3152
Head number	0.0043	0.0166	0.0355	0.0018	0.0693	0.4764
σ_I	61.5295	38.3112	31.2913			
σ_H	96.9824	56.3777	41.4266			
r_{IH}	0.6344	0.6795	0.7533			
$G_{Y_{DOM}}$	18.4k	19.2k	20.3k			
$G_{Y_{GS}}$	36.7k	36.4k	34.9k			

The assignment of different economic weights changed the individual contribution of the variates to the indices. The standard deviation of the index and of the aggregate breeding value and their mutual correlation were affected as well. The standard deviation of the aggregate breeding value was highest in both aggregate breeding values in Set A.

But if these standard deviations were converted into the units of measurement by multiplying σ_I by the regression coefficient of each characteristic on the index, the expected responses in herbage and seed yield, expressed as percentages of their means, did not markedly differ for the different economic values. This was caused by the high genotypic correlations between the two characteristics in the aggregate breeding value. The larger part of the expected response could be accounted for by the variates that exerted the greatest influence on the indices with the 11 variates. The other variates only contributed to a small extent.

The values of the variates time of head emergence and head number differed to a great extent in the indices whose aggregate breeding values comprised either Y_{DM} and Y_{CL} or Y_{DOM}

and Y_{GS}. In the index with the first-mentioned aggregate breeding value, time of head emergence was of minor and head number of major importance (Table 33). In the index with Y_{DOM} and Y_{GS} as aggregate breeding value it was the other way round (Table 34).

The influence of these two variates on each of the two Y-characteristics in the two aggregate breeding values could be deduced from the selection indices whose aggregate breeding value was derived either from herbage yield or seed yield (indices not given). From these indices it was found that the Y-characteristic seed yield was responsible for the reversed situation.

The influence of time of head emergence on the indices with either Y_{DM} or Y_{DOM} as sole Y-characteristic in the aggregate breeding value was similar, as were the genotypic correlation coefficients between these characteristics (Table 32). In the indices with Y_{CL} or Y_{GS} as sole Y-characteristic, time of head emergence had a greater value in the former index than in the latter. In Chapter 3 it was found however that time of head emergence exerted a greater relative influence on $^{10}\log Y_{CL}$ than on $^{10}\log Y_{GS}$ (Table 24), an explanation of which was given in Section 3.3.3. The diverging values of time of head emergence in the two indices could therefore not be accounted for.

In the indices with Y_{CL} or Y_{GS} as sole Y-characteristics, head number exerted a greater influence on the index whose aggregate breeding value was composed of Y_{CL} only than on the index with Y_{GS} as aggregate breeding value. This finding agreed with the results discussed in Section 3.3.3. The difference was due to the absence of a correlation between Y_{CL} and germination percentage on one hand (see Section 3.3.2) and between head number and germination percentage on the other (see Section 3.3.3).

6.3.3 Discussion

Y_{DM} and Y_{CL} were improved by 21 and 31%, respectively (means of genetic gains for three sets of economic weights) at a selection intensity of one standard deviation of the index by the simultaneous selection on both characteristics through 11 X-variates, these gains being 19 and 36% for Y_{DOM} and Y_{GS}, respectively. However, not all the X-variates observed contributed equally to the ultimate response. Fresh weight of the plant at seed harvest proved to be the most important characteristic determining herbage and seed yield. An additional important one was head number when the aggregate breeding value comprised Y_{DM} and Y_{CL}.

From Chapters 2 and 3 it was already evident that fresh weight affected herbage and seed yield to a large extent. In view of the results obtained with the selection indices, it can be concluded that fresh weight influenced both characteristics of the aggregate breeding value in a similar way. Its genotypic and phenotypic correlations with herbage and seed yield (Tables 23 and 32) were high, while its heritability in the wide sense was 0.52. Selection for a high fresh weight at seed harvest seemed fully justified as the aim was to increase both herbage and seed yield.

Fresh weight could only be determined after flowering. If the next step after initial selection is the testing of the open-pollinated progenies, no full parental control on the selected plants is obtained. But if root splits of the selected plants are taken for

planting in a mating scheme to produce an offspring for further evaluation, it makes no difference if the characteristic is observed before or after flowering.

Tiller weight and tiller length showing a strong mutual correlation (Table 8) could be observed before flowering and both variates had a high value in the indices as was found on stepwise elimination of the least influential variates in the two aggregate breeding values. Both characteristics possessed an exceptionally high heritability in the wide sense, while the repeatability of tiller length was negative and that of tiller weight was high (Table 9). With these characteristics selection for both herbage and seed yield could be done before flowering, thus giving control over the male parent as well. Recording the two characteristics is rather cumbersome, however, and the advantages it brings of observing before flowering have to weighed against the disadvantages of the workload involved.

Number of heads was an important tool for improvement of Y_{CL} but, in agreement with the conclusions in Chapter 3, did not have a definite predictive value for Y_{GS}.

6.4 THE OPEN-POLLINATED PROGENY OF THE 121 PLANTS

6.4.1 Material and methods

Open-pollinated seed was harvested from the 121 plants occurring in the spaced-plant population of 4000 plants of Nandi I (see Chapter 1) during the first 1973 crop - all 4000 plants, including the 121, were allowed to contribute to the pollen cloud.

Each plant was harvested individually about seven weeks after its time of head emergence. The seed of the 121 plants was cleaned and about 400 seeds of each plant were laid out on filter paper and covered with bell-jars during January 1974. Two weeks after the first seeds of each plant started to germinate, 30 seedlings per half-sib family were taken at random from the filter paper and planted in wooden boxes.

The progenies were planted at Locations A, B and C in fields approximately 1 km from each other at the National Agricultural Research Station. At each location 8 plants per family were planted 0.75 m apart in plots of 2 rows of 4 plants each. The planting dates for Locations A, B and C were 9 April, 10 April and 15 May, respectively. Three weeks after planting, dead plants (6% of the total) were replaced by spare plants. The experimental lay-out was one replicate of a simple lattice per location.

Each of the three locations had a different history. Location A had been under maize cultivation continuously during the preceeding years until 1973 without high fertilizer inputs (approximately 50 kg of phosphate and 75 kg of nitrogen per hectare). In 1973 this field was ploughed up and sown with silverleaf desmodium for seed production. Location B had been used as an isolation plot for the maize-breeding programme from 1965 until 1973 with high fertilizer inputs (200 kg of phosphate and 200 kg of nitrogen per hectare). In 1973 the land was not cultivated. Location C was under grass, Rhodes grass and *Pennisetum purpureum* Schumach. (Napier grass), and under maize alternately with medium fertilizer inputs (100 kg of phosphate and 150 kg of nitrogen per hectare). The land was ploughed up at the beginning of 1974 and therefore became available rather late, which explained the late planting date.

Approximately two months later (19 June, 21 June and 21 July for Locations A, B and C, respectively) each plant was propagated vegetatively and the half-sib family of eight plants was planted as an identical set in the second replicate of the lattice. Clones were multiplied under very wet conditions and less than 1% of the transplants died, being replaced by root splits taken afresh from Replicate 1.

Each plant received single superphosphate at a rate of 40 kg phosphate per ha at time of planting. The plants were allowed to grow undisturbed for the remainder of the year (Replicate 1 was cut back when the plants were propagated vegetatively) and received a cleaning cut in December.

All plants were top-dressed at a rate of 100 kg of nitrogen per ha on 17, 18 and 19 April 1975. The following observations were made:

- time of head emergence for each plant;
- growth vigour of each plant on a 1-5 scale (5 being the highest) in the week that the first plants in a location had developed 10 or more heads;
- fresh weight at time of seed harvest per family.

The inflorescences were harvested separately for each family as described in Appendix 1. The following data were noted per family:

- number of heads;
- yield of clean seed (Y_{CL});
- % germinating seeds (% GS);
- yield of germinating seeds (Y_{GS}).

The same data were obtained for the second 1975 crop after a cleaning cut and a top-dressing with 100 kg of nitrogen per ha on 17 August.

In 1976, the plants at the three locations were cut and top-dressed at a rate of 100 kg of nitrogen per ha on 13, 16 and 17 April. Owing to a severe drought, all plants were cut back and top-dressed at a rate of 50 kg nitrogen per hectare. At four weeks' regrowth the fresh weight of each plant of Replicate 1 was determined in the three locations. The dry-matter content was determined from the bulk of the eight plants per family per location. Of 50 families chosen at random, D_{vitro} was assessed in the bulk sample. Replicate 2 in each location was cut in eight weeks' regrowth and the same observations were made as for Replicate 1 (the 50 random plants were the same for both replicates). These measurements were repeated twice during 1976 without recording the individual weights after cleaning cuts and top-dressings at a rate of 100 kg of nitrogen per ha on 16 July and 16 September, respectively. The periods of regrowth of Replicate 1 were maintained at four weeks, while those of Replicate 2 were again eight weeks.

The two periods of regrowth per location were taken in order to study the change of D_{vitro} and Y_{DM} with time within families. The results did not add new information to that already given in Chapter 2 and will therefore not be discussed here.

The data recorded on the two crops of the year 1975 were summed per family and replicate for each location. The dry-matter yields of the three harvests per location in 1976 were summed likewise. As the period of regrowth was confounded with replicates, each plot yield was expressed in proportion to the mean of the replicate in which it occurred. The

observed characteristics were analysed within locations and, in a combined form, over locations according to the following models:

within locations:

$$Y_{ijk} = \mu + r_i + b_{j:i} + \underline{f}_k + \underline{e}_{ijk}$$

in which

Y_{ijk} = observation of family k in block j of replicate i
μ = overall mean
r_i = fixed replicate effect; i = 1, 2
$b_{j:i}$ = fixed block effect within replicate i; j = 1, 2 ... 11
$\underline{f}_k$ = random family effect; k = 1, 2 ... 121
$\underline{e}_{ijk}$ = random error

between locations:

$$Y_{jkl} = \mu + \underline{f}_k + \underline{l}_l + (\underline{fl})_{kl} + \underline{e}_{jkl}$$

in which

Y_{jkl} = the j^{th} observation of family k in location l
μ = overall mean
$\underline{f}_k$ = random family effect; k = 1, 2 ... 121
$\underline{l}_l$ = random location effect; l = 1, 2, 3
$(\underline{fl})_{kl}$ = random interaction effect between family and location
$\underline{e}_{jkl}$ = random error

The analysis of variance within locations is presented in Table 35 while Table 36 shows the analysis of variance between locations. The analyses of variance were carried

Table 35. The analysis of variance between families within a location.
r = number of replicates.
b = square root of number of families = number of blocks.
n = number of families.
σ^2_e = error component of variance.
σ^2_g = genotypic variance between families.

Source of variance	Degrees of freedom	Mean squares	Expected mean squares
Replicates	r - 1	MSR	
Blocks within replicates	r(b - 1)	MSB	
Between families corrected for blocks	n - 1	MSF	$\sigma^2_e + \frac{b}{b+1} r \sigma^2_g$
Error	(b-1)(rb-b-1)	MSE	σ^2_e
Total minus correction term	rn - 1		

Table 36. Combined analysis of variance in 1 locations.
n = number of families.
l = number of locations.
r = number of replicates per location.
σ^2_e, = error component of variance.
σ^2_{fl} = variance component due to family x location interaction.
σ^2_l = location component of variance.
σ^2_f = family component of variance.

Source of variance	Degrees of freedom	Mean squares	Expected mean squares
Families	n - 1	MSFF	σ^2_e, + r σ^2_{fl} + lr σ^2_f
Locations	l - 1	MSL	σ^2_e, + r σ^2_{fl} + nr σ^2_l
Families x locations	(n-1)(l-1)	MSI	σ^2_e, + r σ^2_{fl}
Error	nl(r - 1)	MSEE	σ^2_e,
Total minus correction term	nlr - 1		

out according to the least squares analysis of Harvey (1976).

The eight genotypes per half-sib family have been planted in duplicate per location, like clones consisting of two plants. The eight plants of a half-sib family in one replicate can therefore be considered as a clonal replication of the same family in the other replicate at the same location. The analysis of variance within a location has been carried out accordingly. As the fresh weight at seed harvest time, head number, Y_{CL}, Y_{CS} and Y_{DM} of three harvests were not recorded on the individual plants of a family, the variance of a family within a plot could not be determined. From the analysis of variance given in Table 35 the following estimates were made:

- the genotypic variance between families (s^2_g) per location was found to be

$$s^2_g = \frac{MSF - MSE}{1.83} \quad (b = 11,\ r = 2)$$

- the environmental variance per location (s^2_e) (including the variance within a plot)

$$s^2_e = MSE$$

- the heritability in the wide sense (h^2_w) between half-sib families per location was

$$h^2_w = \frac{s^2_g}{s^2_g + s^2_e}$$

- the heritability in the wide sense over 3 locations, calculated from the average genotypic and environmental variances of three locations.

In the analysis of variance of 3 locations (Table 36) a two-way classification was carried out in accordance with the classification families and locations, with two observations per cell. The following estimates were made:

- the family component of variance (s_f^2) was found as

$$s_f^2 = \frac{MSFF - MSI}{6} \quad (l = 3,\ r = 2)$$

- the location component of variance (s_l^2) as

$$s_l^2 = \frac{MSL - MSI}{242} \quad (n = 121,\ r = 2)$$

- the interaction component of variance (s_{fl}^2) as

$$s_{fl}^2 = \frac{MSI - MSEE}{2} \quad (r = 2)$$

- the error component of variance ($s_{e'}^2$) as

$$s_{e'}^2 = MSEE$$

- the additive genetic variance of families (s_a^2) as

$$s_a^2 = 4\, s_f^2 \quad \text{(Falconer, 1960)}$$

- the heritability in the narrow sense (h_n^2) as

$$h_n^2 = \frac{s_a^2}{s_f^2 + s_l^2 + s_{fl}^2 + s_{e'}^2}$$

Time of head emergence and growth vigour in 1975 and Y_{DM} of the first harvest of 1976 were determined on individual plants. The plots of a half-sib family in replicates 1 and 2 within a location were identical. When analyzing the plot totals, leaving out of consideration genotypical and environmental differences between plants within families, the error component of variance was similar in MSE and MSF (Table 35). But, if the individual plants of a family are taken into account in the analysis, the plants in the two plots of one family are not independent random samples, as will be outlined below.

Variation of plot means of identical sets of eight clones amounts to

$$\sigma_p^2/8 \qquad (10)$$

The variation of families, for sums of (two) means of identical sets of eight clones, equals

$$\frac{2}{8}\sigma_p^2 + 2\frac{2\sigma_{cl}^2}{8} + 2^2\sigma_{fam}^2 = \frac{2}{8}\sigma_p^2 + \frac{1}{2}\sigma_{cl}^2 + 4\sigma_{fam}^2 \qquad (11)$$

where

σ_{cl}^2 refers to the clonal component of variation of plants within plots, and

σ_{fam}^2 is the family component of variation of plants from different families.

Expressions (10) and (11) can be simplified to a 'per plant' basis as

$$\sigma_p^2 \quad \text{(within clones)} \qquad (12)$$

and

$$\sigma_p^2 + 2\sigma_{cl}^2 + 16\sigma_{fam}^2 \quad \text{(between families)} \qquad (13)$$

Considering the plot totals, expressions (12) and (13) have to be multiplied by 8, which leads to $8\sigma_p^2 = \sigma_1^2$ and $8\sigma_p^2 + 16\sigma_{cl}^2 + 128\sigma_{fam}^2 =$

$$\sigma_1^2 + 16\sigma_{cl}^2 + 2\sigma_g^2 = \sigma_2^2 + 2\sigma_g^2,$$

in which

σ_1^2 = the variation of plot totals for plots with identical sets of clones

σ_2^2 = the variation of plot totals with random choice of clones per plot

σ_g^2 = the component of total plot variation due to genotypic variation of families

In a generalised form, σ_2^2 can be written as

$$\sigma_2^2 = \sigma_1^2 + rm\sigma_{cl}^2,$$

in which

r = the number of replicates and

m = the number of plants per plot

The expected mean squares of MSF and MSE were thus:

$$\varepsilon MSF = \sigma_2^2 + \frac{11}{12}\cdot 2\sigma_g^2$$

$$\varepsilon MSE = \sigma_1^2,$$

in which

$$\sigma_2^2 = \sigma_1^2 + 16\sigma_{cl}^2$$

The clonal component of plant variation for family j ($\sigma^2_{cl(j)}$) can be estimated with

$$\hat{\sigma}^2_{cl(j)} = \frac{\frac{\sum_{i=1}^{8} s_{ij}^2 - \frac{\left(\sum_{i=1}^{8} s_{ij}\right)^2}{8}}{7} - \frac{\sum_{i=1}^{8} d_{ij}^2 - \frac{\left(\sum_{i=1}^{8} d_{ij}\right)^2}{8}}{7}}{4}$$

in which

s_{ij} = the sum of the observations on plants of clone i of family j in replicates 1 and 2

d_{ij} = the difference between the observations on plants of clone i of family j in replicates 1 and 2

An unbiased estimator of the clonal component of plant variation ($\hat{\sigma}^2_{cl}$) can then be obtained with

$$\hat{\sigma}^2_{cl} = \frac{\sum_{j=1}^{121} \hat{\sigma}^2_{cl(j)}}{121}$$

The genetic component of variance (s^2_g) is estimated with

$$s^2_g = \frac{MSF - (MSE + 16\hat{\sigma}^2_{cl})}{\frac{11}{12} \times 2}$$

6.4.2 Results

The means per plant and per harvest, the genotypic and error components of variance, the heritability in the wide sense on a family basis and the coefficients of variation of the seven measured characteristics are given per location and as a mean of three locations in Table 37, calculated from the analysis of variance shown in Table 35. At each location, differences between families were significant for all characteristics ($P < 0.01$).

Table 38 gives the components of variance and the heritability in the narrow sense, calculated in accordance with the analysis of variance given in Table 36. Differences between families and between locations were significant for all characteristics ($P < 0.01$), except for Y_{DM}, for which no location effect could be calculated as its values were expressed relative to the means of the replicates. Time of head emergence and Y_{DM} displayed a significant family x location effect ($P < 0.01$) - no significant interaction occurred for the other characteristics.

Location A, which had been under maize cultivation continuously without high fertilizer inputs (see Section 6.4.1), showed the lowest herbage and seed yields compared with

Table 37. Means of characteristics, components of variance (s_g^2 and s_e^2), heritability in the wide sense (h_w^2) and coefficients of variation (% CV) per location and averaged over locations.

Characteristic	Location	Means per plant and per harvest	s_g^2	s_e^2	h_w^2	% CV
Time of head emergence (weeks)	A	3.1	67.0773	71.3326	0.48	15.9
	B	2.2	48.4056	28.0093	0.63	15.2
	C	2.9	63.0459	25.0044	0.72	10.7
	Mean	2.7	59.5096	41.4488	0.59	
Growth vigour	A	3.5	15.9616	16.2665	0.50	7.2
	B	3.5	10.3717	8.9854	0.54	5.3
	C	3.3	6.3946	11.8252	0.35	6.5
	Mean	3.4	10.9093	12.3590	0.47	
Fresh weight (kg)	A	1.88	5.0431	8.5565	0.37	9.7
	B	2.03	4.5560	9.1549	0.33	9.3
	C	2.39	10.3642	11.8147	0.47	9.0
	Mean	2.10	6.6544	9.8420	0.40	
Head number	A	62	6398.3545	42502.5372	0.13	20.7
	B	58	8054.8676	20628.3911	0.28	15.4
	C	52	5533.8135	18275.9551	0.23	16.2
	Mean	57	6662.3452	27135.6278	0.20	
Y_{DM} [1]	A	129	57.4317	100.8906	0.36	10.1
	B	181	31.1744	64.0463	0.33	8.0
	C	151	73.1193	151.0790	0.33	12.3
	Mean	154	53.9085	105.3386	0.34	
Y_{CL} (g)	A	1.96	17.7815	87.6207	0.17	36.2
	B	2.28	42.0023	65.0931	0.39	21.7
	C	2.52	33.1127	82.7222	0.29	23.2
	Mean	2.25	30.9655	78.4787	0.28	
Y_{GS} (g)	A	0.59	2.4407	22.7678	0.10	50.5
	B	0.67	5.7430	20.9286	0.22	42.6
	C	0.74	5.6900	15.6585	0.27	33.6
	Mean	0.67	4.6246	19.7850	0.19	

1. Means are expressed in absolute values (g), while analysis of variance is calculated for relative figures.

Table 38. Components of variance (s_f^2, s_a^2, s_l^2, s_{fl}^2 and $s_{e'}^2$) and heritability in the narrow sense (h_n^2) of the combined analysis of variance of 3 locations.

Characteristic	s_f^2	s_a^2	s_l^2	s_{fl}^2	$s_{e'}^2$	h_n^2
Time of head emergence	32.5510	130.2040	84.0078	27.1947	44.5055	0.69
Growth vigour	3.3072	13.2288	3.5622	0.8882	26.8333	0.38
Fresh weight	3.0919	12.3676	17.3585	1.2395	15.1448	0.34
Head number	5120.4270	20481.7080	6366.6413	895.2451	30826.2176	0.47
Y_{DM}	22.5566	90.2264	-	28.7237	161.2011	0.42
Y_{CL}	21.6050	86.4201	20.2768	3.4709	96.1235	0.61
Y_{GS}	3.5745	14.2979	1.2567	0.6661	21.2909	0.53

the other two locations. The lower fresh weight at seed harvest was corroborated by the lower seed yield, and confirmed the previously reported correlation between these two characteristics (Chapter 3 and Section 6.3). Time of head emergence at Location A was, on average, later than that of B and C, which indicated a slower growth rate at Location A, with lower herbage and seed yields. The number of heads was not affected so much. Location B, having been under high fertilizer inputs, was earliest in head emergence. This characteristic was stressed further by the higher dry-matter yield at Location B in the year subsequent to recording time of head emergence, owing to the quick regrowth after the cleaning cut, especially after four weeks' regrowth at the beginning of the growing season. At later stages of growth this initial superiority was not evident, as is clear from the lower fresh weight at seed harvest at Location B compared to Location C.

In addition to the lower yields, Location A, apart from Y_{DM}, showed the highest coefficient of variation compared with the other locations, indicating the higher heterogenity in soil conditions of that location.

The estimated heritabilities in the wide sense of time of head emergence and fresh weight (Table 37) were lower than those of the parent population (Table 9), while the heritabilities of head number, Y_{CL} and Y_{GS} fell far below the values shown in Table 22 for the parent population. Y_{DM}, in contrast, displayed approximately similar heritabilities in the parent population (see Section 2.3.2) and the offspring. The heritability in the wide sense was calculated from the variance between identical families in the two replicates, based on the plot totals of the eight plants. The error variance on all eight plants will be greater than on single plants, resulting in a lower heritability of the offspring than the parents.

The largest component of the total observed variance of growth vigour, head number, Y_{DM}, Y_{CL} and Y_{GS} was found to be the error component of variance (Table 38). Location differences were the biggest source of variance for time of head emergence. For fresh weight, both location and error component were large contributors to the total variance. The interaction component was relatively small compared to the other components of variance.

Time of head emergence showed the greatest heritability in the narrow sense of the observed characteristics (Table 38), as was the case with heritability in the wide sense of this characteristic as well (Table 37). Y_{CL} and Y_{GS} showed high values for the heritability in the narrow sense, higher than the remaining characteristics in Table 38. This was not in agreement with the results presented in Table 37, in which these two characteristics exhibited relatively low heritability values in the wide sense. The high family component of variance of Y_{CL} and Y_{GS}, when analysed over locations, must be held responsible for this reversed situation. The absolute values of heritability in the wide and the narrow senses, as presented in Tables 37 and 38, respectively cannot be compared as they were obtained in two different ways.

The analysis of variance of individual plants per family for the time of head emergence, growth vigour and Y_{DM} characteristics yielded information on the size of the variance within plots, that is genotypic differences between plants within families, compared to the genotypic variance between families. These two components are presented in Table 39 together with their ratio.

For time of head emergence the genotypic variance between families was on average

10.3 times as large as the variance between plants within plots. Selection for this characteristic on a family basis therefore seems significant. There was greater variance for time of head emergence between families in the first crop than in the second, while the variance within plots was approximately the same for both crops. The large inter-family variation was caused by the skew distribution of time of head emergence of the individual plants, being more pronounced between families than within them. The skewness was caused by the high growth rate at the onset of the rains after the dry season (see Chapter 1) when most of the plants produce heads within a short time. Head emergence of late-heading plants then takes place over an even longer period because of the strong competition from the early-heading plants. In the second crop, heading is more evenly distributed because of the lower rainfall.

Growth vigour, which was visually rated on a 1-5 scale, displayed a genotypic variance between families, which was on average 5.6 times as great as the variance within plots. When selecting for this characteristic, family selection should be applied. At Location A the ratio between s_g^2 and s_{cl}^2 was large in comparison with the other two locations. This was caused by the larger genotypic component of variance at Location A. Under the poorer soil conditions of this location, extremes between families were more distinct.

Only at Location A was the genotypic component of variance of Y_{DM} 4.5 times larger than the variance within plots, while at the other locations the latter was greater than the variance between families. This indicated that mass selection should be applied when selecting for Y_{DM}, as the differences between families were less than those within families at two locations.

The variance between plants within plots was compared with the average time of head emergence per family. It was found that the late-heading families showed wider variation in heading time than early-heading families (data not presented).

6.4.3 Discussion

The offspring under study originated from 121 unreplicated plants that were randomly chosen from the spaced-plant population of 4000 plants of the variety Nandi I. A wide range in heading dates was observed in the sub-population of 121 plants (Table 7) and in the popu-

Table 39. Genotypic variances between families (s_g^2) and variances within plots (s_{cl}^2).

Character	Location	1 st crop of 1975			2nd crop of 1975			1st crop of 1976		
		s_g^2	s_{cl}^2	s_g^2/s_{cl}^2	s_g^2	s_{cl}^2	s_g^2/s_{cl}^2	s_g^2	s_{cl}^2	s_g^2/s_{cl}^2
Time of head emergence	A	18.8008	1.2918	14.6	8.3617	1.8562	4.5			
	B	17.1698	1.2151	14.1	7.9764	0.6959	11.5			
	C	10.4138	0.6241	16.7	5.8129	0.9981	5.8			
Growth vigour	A	2.6437	0.2185	12.1	1.5279	0.2530	6.0			
	B	0.8960	0.2140	4.2	0.8537	0.1784	4.8			
	C	0.7243	0.2032	3.6	0.6389	0.2416	2.6			
Yield of dry matter	A							1195.7495	263.1592	4.5
	B							-[1]	286.5833	-
	C							-[1]	503.7538	-

1. $s_g^2 < 0$

lation of 4000 plants (Boonman & Van Wijk, 1973). Besides the extended period of head emergence in tropical grasses, prolonged head formation over a period of up to three months in single plants occurred as well (Boonman, 1971a). Moreover, anthesis and stigma exsertion in setaria were found to continue for seven weeks within single plants (Boonman, 1971a). This applied especially to early-heading plants; late-heading plants flowered for a shorter time. Heads that emerged early thus flowered over a longer period than those that emerged late.

Because of these factors it was assumed that, in spite of the variation in head emergence of the 121 plants, most plants, apart from the very early-heading ones, contributed simultaneously to the pollen cloud.

Wit (1952) found in perennial ryegrass that plants were fertilized on average to 40% by adjacent plants and to 22, 12, 11, 7, 5 and 4%, respectively by next nearest plants. Bogdan (1963) investigated the contamination of clones of Rhodes grass, characterized by purple coloration on the spikelets, the racemes of the panicle, the nodes of the stem, the lower leaf-sheaths and on the coleoptile in the seedlings, in a population of the same species without anthocynanin coloration. This last characteristic was found to be recessive and homozygous. The purple clones surrounded a plot of anthocyanin-free plants of 30 x 14 m. Up to 30% purple seedlings could be found in the progenies of individually harvested anthocyanin-free plants at a distance of 5 meter from the purple plants and up to 10% at 11 meters. Pollen of the purple plants were thus carried over long distances. It has to be realised, however, that abundant pollen of the purple plants was available due to the large number of plants surrounding the plot.

Because of these neighbour effects no homogeneous pollen cloud could have been produced in the population of 121 plants and assortative mating must have occurred between neighbouring plants of different order. This effect however was reduced by the long duration of flowering of the 121 plants for which reason fertilization was restriced not only to near neighbours. It was quite common to find flowering and seed shedding in the same head as well as abundant flowering at the optimum date of harvesting.

Comstock & Robinson (1952) gave the assumptions underlying the derivation of the mean squares expectations and the genetic interpretation of cross-pollinating crops:

a) random choice of individuals mated for the production of experimental progenies;
b) random distribution of genotypes relative to variations in environment;
c) no non-genetic maternal effect;
d) regular diploid behaviour at meiosis;
e) no linkage;
f) no multiple alleles;
g) no epistasis.

Condition (a) had been met as the population of 121 plants was randomly chosen out of the source population of 4000 plants of Nandi I (Chapter 1). The 4000 plants were obtained at random from a seed-production field of Nandi I and were planted as spaced plants without any prior classification.

Condition (b) was valid because of the use of proper randomization techniques.

Condition (c), no non-genetic maternal effect, might not be completely valid because of maternal inheritance through the cytoplasma of the maternal half-sibs and because of the

effects from seed size of parents and progenies.

Condition (d), regular diploid behaviour in the case of meiosis, was met because of the diploid character of setaria.

Condition (e), no linkage, could imply a linkage equilibrium. The Nandi ecotype was introduced out of the local flora in 1935 and was maintained in a plot of 400 square meters (Chapter 1). It is not known whether this came about through vegetative material raised from the first bulking up of seed of the original introduction or through continuous seed multiplication. When the Nandi ecotype came into commercial production in 1957 it was multiplied continuously from harvest to harvest without maintenance of the original seed stock. It can therefore be assumed that the population used for the foundation of the source population of the Nandi ecotype was in linkage equilibrium.

No opinion can be given on conditions (f) and (g), the absence of multiple alleles and epistasis.

By testing plant material at one location only, the genotype × location interaction component of variance cannot be differentiated from the genotypic variance of the plant material. Both components of variance are confounded, which will lead to over-estimation of the genotypic variance. However, the 121 half-sib progenies were evaluated at three locations, so that an estimate of the family × location component of variance was obtained. The genotypic component of variance was also estimated at each location, and it consisted of additive variance, dominance variance, epistasis variance and variance due to family × location interaction. The dominance variance could not be estimated as no full sibs were precised within the half-sib families and no opinion could be given on epistasis variance. The remaining components were estimated and the relationship between these components was

$$\bar{s}_g^2 = s_f^2 + s_{fl}^2,$$

in which

$\bar{s}_g^2$ = the mean of the genotypic variance of the families at the three locations, estimated from the analysis of variance presented in Table 35

s_f^2 = the family component of variance estimated from the analysis of variance given in Table 36

s_{fl}^2 = the interaction component of variance between families and locations, estimated from the analysis of variance shown in Table 36.

When applied to the components of variance given in Tables 37 and 38 this relationship was approximately true for the characteristics time of head emergence, head number, Y_{DM} and Y_{GS}, but differed to a large extent for growth vigour and fresh weight and to a lesser extent for Y_{CL}. In all cases the sum of s_f^2 and s_{fl}^2 was smaller than $\bar{s}_g^2$. The part of the genotypic variance that could not be accounted for by s_f^2 and s_{fl}^2 must have been caused by variance due to dominance and by family × location interaction, which was not adequately covered by s_{fl}^2. This was especially true for growth vigour, fresh weight of the plant at seed harvest and Y_{CL}.

The fresh weight of the plant at seed harvest, which proved to be an indicator of

the growth vigour of a plant at its time of head emergence (see Section 3.3.3) displayed large location-and-error components of variance. This might have been caused by inaccuracies arising from evaluation of herbage yield on a fresh-weight basis only (e.g. the presence of dew, time of day when sampled), though Y_{DM} also showed a large error component. Boonman & Van Wijk (1973) suggested that setaria plants do not produce heads in any appreciable quantity until a minimum of herbage has accumulated. Because of this latter contention and the large location-and-error-variance components of fresh weight, the interaction between family and location for time of head emergence is significant. When determining time of head emergence of setaria plants, the material should therefore be evaluated at different locations.

Y_{DM} also showed a significant family × location interaction. This characteristic showed a large variation and from the analysis of the individual plants it was found that for two locations the variation within families was greater than between families. This characteristic, like fresh weight, is very much affected by environmental influences and the observed significant interaction is a reflection of this.

In the analysis of variance, carried out in accordance with Table 35, the plot totals were analysed without considering the variation present within plots of eight plants. For time of head emergence, growth vigour and Y_{DM} the variation within plots was also taken into account by calculating s^2_{cl}. Heritabilities in the wide sense for these characteristics were calculated for the eight plants per family (if $s^2_g > s^2_{cl}$) from

$$h^2_w = \frac{s^2_g}{s^2_l + s^2_{cl} + s^2_g}$$

The heribatilities calculated in this way (data not presented) were lower than those presented in Table 37. This was caused by the lower estimate of the genotypic variance that occurred in the numerator and the higher value of the denominator due to the inclusion of the clonal component of plant variation. The analysis presented in Table 35 has therefore led to an overestimation of the heritability in the wide sense as the clonal component of variation within plots was confounded with the genotypic variance.

The greater variation in time of head emergence shown in late-heading compared to early-heading families indicated the presence of early heading plants in late families. But the variation was not so large as to make s^2_{cl} greater than s^2_g. Especially when a check is made for varietal purity in seed-multiplication plots, late-heading varieties can be more easily rejected when early-heading plants are present than the other way round. The former come more to the foreground than the latter.

6.5 SELECTION INDICES ESTIMATED FROM THE PARENT-OFFSPRING RELATIONSHIP

6.5.1 Material and methods

The following characteristics of the parent population were to be included in the selection indices estimated from the parent-offspring relationship:

- tiller number;
- time of head emergence;
- tiller angle;
- tiller length;
- leaf number;
- leaf width;
- leaf length;
- stem diameter;
- tiller weight;
- fresh weight of the plant at seed harvest;
- head number;
- Y_{DM};
- Y_{DOM};
- Y_{CL};
- Y_{GS}.

These characteristics are described in Appendix 1, and their recording is outlined in Sections 2.2.1 and 3.3.1. The means, averaged over harvests and corrected for blocks, were used.

The following characteristics of the offspring, as described in Appendix 1 and recorded as described in Section 6.4.1, were used for the estimation of the selection indices:

- time of head emergence;
- fresh weight of the plant at seed harvest;
- head number;
- Y_{DM};
- Y_{CL};
- Y_{DOM} of 50 randomly chosen plants;
- Y_{GS}.

The block-corrected means of the offspring were averaged over crops and locations.

Heritabilities in the narrow sense (h_n^2) of the characteristics recorded in both the parent population and its offspring were calculated as twice the regression of the offspring on the maternal parent. The standard error of the heritability (SE (h^2)) was calculated according to Becker (1975) as

$$SE\ (h^2) = 2\sqrt{\frac{\Sigma\ z^2 - \frac{(\Sigma\ xz)^2}{\Sigma\ x^2}}{(N - 2)\ \Sigma\ x^2}}$$

in which

$$\Sigma\ x^2 = \Sigma\ X^2 - \frac{(\Sigma\ X)^2}{N}$$

$$\Sigma\ z^2 = \Sigma\ Z^2 - \frac{(\Sigma\ Z)^2}{N}$$

$$\Sigma xz = \Sigma XZ - \frac{\Sigma X \Sigma Z}{N}$$

X = parent values
Z = offspring values
N = number of half-sib families

Genotypic correlations (r_g) between the characteristics evaluated in the parent population and the offspring were determined according to Becker (1975) as

$$r_g = \frac{cov_{X_1Z_2} + cov_{X_2Z_1}}{2\sqrt{cov_{X_1Z_1} \cdot cov_{X_2Z_2}}}$$

in which

$cov_{X_1Z_2}$ = covariance of characteristic 1 in the parent X and characteristic 2 in the offspring Z

$cov_{X_2Z_1}$ = covariance of characteristic 2 in the parent X and characteristic 1 in the offspring Z

$cov_{X_1Z_1}$ = covariance of characteristic 1 in the parent X and characteristic 1 in the offspring Z

$cov_{X_2Z_2}$ = covariance of characteristic 2 in the parent X and characteristic 2 in the offspring Z

The standard error of the estimated genotypic correlation (SE (r_g)) (Falconer, 1960) is approximately

$$SE\ (r_g) = \frac{1 - r_g^2}{\sqrt{2}} \sqrt{\frac{SE(h_1^2)SE(h_2^2)}{h_1^2\ h_2^2}},$$

in which

r_g = genotypic correlation between characteristics 1 and 2
$SE(h_1^2)$ = standard error in the heritability of characteristic 1
$SE(h_2^2)$ = standard error in the heritability of characteristic 2
h_1^2 = heritability of characteristic 1
h_2^2 = heritability of characteristic 2

Family means for the heritability and genotypic correlation estimations were calculated on a plant basis by dividing the plot totals, averaged over crops and locations, by 8. The heritability and genotypic correlations of Y_{DOM} were determined for the 50 families and their corresponding parents.

The phenotypic correlations (r_{ph}) between the characteristics were calculated from the parent population as

$$r_{ph} = \frac{cov_{X_1X_2}}{\sqrt{var_{X1} \cdot var_{X2}}}$$

in which

$cov_{X_1X_2}$ = covariance of characteristics 1 and 2 of the parent X
var_{X_1} = variance of characteristic 1 of the parent X
var_{X_2} = variance of characteristic 2 of the parent X

The breeding value of half-sib families is defined as twice the mean deviation of the family mean from the population mean (Falconer, 1960). According to De Wolff (1972) the expected aggregate breeding value may be estimated through the multiple regression of the progeny means of the observed aggregrate breeding value H (dependent characteristics) on the parent characteristics of the index I (independent variates).

Selection indices were estimated in accordance with De Wolff (1972) using herbage and seed yield as aggregate breeding values. Selection indices with Y_{DOM} as independent characteristic were based on 50 plants and families. Selection indices, composed of the weighted sum of herbage and seed yield were not estimated, as the two characteristics were unequal quantities and their sum would therefore be insignificant.

The selection of equations with a smaller number of independent variates than the full equation but fitting the dependent data as well, was carried out according to the method of Daniel & Wood (1971) and described in Appendix 2.

The response to selection G was estimated from Equation 6 as

$$G = k\, r_{(I,H)}\, \sigma_H$$

in which

k = selection intensity
$r_{(I,H)}$ = correlation between the calculated phenotypic value (I) and the breeding value (H)
σ_H = the standard deviation of the breeding value (H)

An estimate of the correlation between I and H was obtained from the multiple correlation coefficient between the progeny yield and the characteristics of the parent population, while the standard deviation of H was given by twice the standard deviation of the observed yield characteristics of the offspring.

Selection indices were also devised that contained only the variables evaluated in both the parent and offspring populations. An estimation of the heritability in the narrow sense of the index was determined as twice the regression of the index values of the offspring on the index values of the parents obtained from the phenotypic values of parents and offspring.

6.5.2 Results

Table 40 gives the heritabilities in the narrow sense of the measured characteristics with their respective standard errors. Time of head emergence showed the highest heritability, in agreement with the earlier estimated heritabilities (Tables 37 and 38). Fresh weight, head number, Y_{DM}, Y_{DOM} and Y_{CL} were found to have considerably lower values than was previously calculated (Table 38).

The phenotypic correlations were estimated from the parent population, whose characteristics had been observed from single plants during three successive crops at one location. The genotypic correlations were determined from both parents and offspring - the former observed during three successive crops, the latter on a family basis consisting of eight plants, during two successive harvests at three locations. In spite of the more intensive testing of the offspring, a similar unbiased estimate of the phenotypic and genotypic correlation was obtained, as will be outlined below.

The genotypic correlation (r_g) between characteristics 1 and 2 obtained in the parent population (X) and the offspring (Z), respectively can be approximated by cov (X_1,Z_2). When Z is measured at n locations, this approximation becomes

$$\text{cov}\ (X_1, \frac{1}{n}\sum_{i=1}^{n} Z_{2i}) = \frac{1}{n}\ \text{cov}\ (X_1, \sum_{i=1}^{n} Z_{2i}) =$$

$$\frac{1}{n}\ \{\text{cov}\ (X_1,Z_{21}) + \text{cov}\ (X_1,Z_{22}) + \ldots\ \text{cov}\ (X_1,Z_{2n})\}.$$

Assume cov (X_1,Z_{21}) = cov (X_1,Z_{22}) = ... = cov (X_1Z_{2n}) = cov (X_1,Z_2),

then cov (X_1,Z_{21}) + ... cov (X_1,Z_{2n}) = n cov (X_1,Z_2).

From this it follows that $r_g \approx \text{cov}\ (X_1, \frac{1}{n}\sum_{i=1}^{n} Z_{2i}) = \text{cov}\ (X_1,Z_2)$.

The phenotypic correlation (r_{ph}) is approximated by cov (X_1,X_2), which corresponds to the last expression of r_g.

Table 40. Heritabilities in the narrow sense (h_n^2) and their standard errors (SE(h_n^2)).

Characteristic	h_n^2	SE (h_n^2)
Time of head emergence	0.545	0.060
Fresh weight	0.159	0.071
Head number	0.109	0.029
Y_{DM}	0.122	0.039
Y_{DOM}	0.180	0.043
Y_{CL}	0.117	0.027
Y_{GS}	0.195	0.064

In Table 41 the genotypic and phenotypic correlations are shown. The phenotypic correlations differed to a slight extent from those presented in Tables 8, 23 and 32 and in Section 6.3.2 which were estimated from the analysis of covariance, while the ones presented in Table 41 were obtained from the means of the parent and offspring characteristics.

Early-heading plants had a higher Y_{CL} than late-heading plants (r_g = -0.398, Table 41), caused mainly by the high genotypic correlation between time of head emergence and head number on one hand (r_g = -0.862), and the positive correlation between Y_{CL} and head number on the other (r_g = 0.363).

This, however, did not lead to a correlation between time of head emergence and Y_{GS} (r_g = 0.003). Similar relationships have been encountered in the parent population (Chapter 3). The correlation between time of head emergence and % germination was calculated for the two crops from each location: the simple correlation coefficients (degrees of freedom = 119) between these two characteristics amounted to -0.031, 0.162 and 0.276 for Locations A, B and C in the first crop, respectively while the correlation coefficients were 0.174, 0.042 and 0.004, respectively in the second crop. The higher Y_{CL} of early-heading plants was therefore levelled off, resulting in smaller differences between early-heading and late-heading plants in terms of Y_{GS}.

The selection of early-heading families will thus improve Y_{CL}, but will not necessarily result in increased herbage yield in spite of the high genotypic correlations between herbage and seed yield, due to the very low genotypic correlation between time of head emergence and the herbage-yield characteristics fresh weight, Y_{DM} and Y_{DOM} (Table 41). Families that combined high herbage and seed yields were to be found in all maturity groups.

The high correlation between herbage and seed yield observed in the parent population (Section 6.3.2) was corroborated by the parent-offspring relationship (Table 41). Fresh weight, obtained at the time of seed harvesting, had a high predictive value for herbage yield, which was determined at set periods of regrowth and seed yield. The genotypic correlations of fresh weight with Y_{DM} and Y_{DOM} exceeded 1 (the correlation coefficients were 1.115 and 1.317, respectively). Because of the close resemblance between both characteristics the genotypic correlation could be expected to be almost 1, thus the chance of calculating a value greater than 1 was great.

Table 42 gives the simple correlation coefficients between the herbage and seed-yield characteristics of the offspring and the characteristics of the parent population. Tiller length, tiller weight and fresh weight showed a higher correlation with herbage yield of the offspring than Y_{DM} and Y_{DOM} by themselves, resulting in a higher response than when selecting directly for Y_{DM} and Y_{DOM}. The highest response for Y_{DOM} was expected from Y_{GS}, which also showed the highest correlation with Y_{DOM} of the 13 characteristics of the parent population. It has to be realised that the responses for Y_{DOM} were based only on 50 plants, which might bias the comparison with the response for Y_{DM} based on 121 plants.

The highest response for seed yield was expected from direct selection for seed yield - the expected response for Y_{CL} and Y_{GS} by selecting these two characteristics amounted to 5.3k and 10.4k, respectively. Fresh weight and Y_{DOM} also showed high expected responses for Y_{GS}. The response of the various characteristics of the parent population differed

Table 41. Genotypic correlations (r_g) and phenotypic correlations (r_{ph}) and the standard errors of r_g. First line : r_g; second line: r_{ph}.

	Fresh weight	Y_{DM}	Y_{DOM}	Head number	Y_{CL}	Y_{GS}
Time of head emergence	-0.047 ± 0.156 -0.273	-0.033 ± 0.131 -0.159	0.039 ± 0.171 -0.169	-0.862 ± 0.031 -0.515	-0.398 ± 0.096 -0.386	0.003 ± 0.134 -0.073
Fresh weight	-	-[1] 0.824	-[1] 0.862	0.231 ± 0.230 0.635	0.764 ± 0.095 0.719	0.932 ± 0.036 0.620
Y_{DM}		-	-	0.317 ± 0.183 0.517	0.714 ± 0.094 0.591	0.937 ± 0.028 0.617
Y_{DOM}			-	0.272 ± 0.245 0.564	0.613 ± 0.025 0.619	0.973 ± 0.014 0.403
Head number				-	0.363 ± 0.153 0.562	0.304 ± 0.189 0.423
Y_{CL}					-	-
Y_{GS}						-

1. $r_g < 1$

Table 42. Simple correlation coefficients (r) between Y_{DM}, Y_{DOM}, Y_{CL} and Y_{GS} of the offspring and the characteristics of the parent population and the improvement in yield expressed as a percentage of the mean yield of the parents (G). k = selection intensity.

Characteristics of the parent population	Y_{DM}		Y_{DOM}[1]		Y_{CL}		Y_{GS}	
	r	G	r	G	r	G	r	G
Tiller number	0.169	1.8 k	0.139	2.0 k	0.163	2.4 k	0.165	6.4 k
Time of head emergence	0.040	0.4 k	0.093	1.3 k	- 0.043	- 0.6 k	0.068	2.6 k
Tiller angle	0.084	0.9 k	0.053	0.8 k	0.024	0.4 k	- 0.007	- 0.3 k
Tiller length	0.370 **	4.0 k	0.473 **	6.9 k	- 0.046	- 0.7 k	0.140	5.4 k
Leaf number	0.190 *	2.1 k	0.131	1.9 k	- 0.075	- 1.1 k	0.163	6.3 k
Leaf width	0.100	1.1 k	0.172	2.5 k	- 0.030	- 0.4 k	0.090	3.5 k
Leaf length	0.175	1.9 k	0.270	3.9 k	0.067	1.0 k	0.062	2.4 k
Stem diameter	0.072	0.8 k	0.145	2.1 k	- 0.007	- 0.1 k	- 0.033	- 1.3 k
Tiller weight	0.320 **	3.5 k	0.393 **	5.7 k	- 0.029	- 0.4 k	0.163	6.3 k
Fresh weight of the plant	0.374 **	4.1 k	0.362 **	5.2 k	0.127	1.9 k	0.187 *	7.2 k
Head number	0.142	1.5 k	0.149	2.2 k	0.118	1.7 k	0.092	3.6 k
Y_{DM}	0.279 **	3.0 k	-	-	0.150	2.2 k	-	-
Y_{DOM}	-	-	0.355 **	5.1 k	-	-	0.201[1]*	7.8 k
Y_{CL}	0.280 **	3.0 k	-	-	0.364 **	5.3 k	-	-
Y_{GS}	-	-	0.547 **	7.9 k	-	-	0.270 **	10.4 k

1. Based on 50 plants and families
* $P < 0.05$
** $P < 0.01$

for Y_{CL} and Y_{GS}: from some of them a negative response in Y_{CL} was expected, whereas the same characteristics showed a positive response for Y_{GS}. The germination percentage of the clean seed must be held responsible for the reversed responses.

From these results it was found that selection towards improved Y_{DM} could be carried out through indirect selection on the fresh weight of the plant at seed harvest, which would simultaneously and positively affect Y_{DOM}. Selection for improved seed yield should be carried out through direct selection for seed yield.

Selection indices with the characteristics of the parent population as independent variables and Y_{DM}, Y_{DOM}, Y_{CL} and Y_{GS}, respectively as dependent variables, are presented in Table 43.

The scatter diagram of the residuals versus the fitted y-values of the four equations exhibited an even distribution of the residuals around the zero line and no transformations of the dependent variables were required. From each equation several subsets of variables were chosen (presented in Appendix 4) that met the requirements of a smaller residual mean square than the full equation and close C_p and p-values.

Each full equation and its subset equations will be discussed below.

Y_{DM} as a dependent characteristic The F-value of the regression equation was significant ($P < 0.01$) and the largest influence on Y_{DM} was exerted by the variate fresh weight of the plant, whose t-value was significant ($P < 0.05$). Other characteristics with a relatively large influence were tiller angle, tiller length and Y_{DM}, but their contributions to the explanation of the dependent variable were not however significant.

Tiller angle and fresh weight were included in the basic set at $C_p = 3.7$ and $p = 3$ with RMS = 73.5379. Six equations of subsets of variates were selected that met the preset conditions. The response to selection of the equation containing all variates expressed as a percentage of the mean dry-matter yield of the 121 parents, was 5.2k, while the response from the subsets of variates was 4.5k and 4.6k.

The response of fresh weight alone was 4.1k. The inclusion of other variates besides fresh weight therefore only contributed to a very small extent to the reduction of the total sum of squares of the dependent characteristic.

Y_{DOM} as a dependent characteristic The equation containing all variates was characterized by a non-significant F-value. Fresh weight displayed the largest influence on Y_{DOM} of the offspring, closely followed by tiller length - the effect of both characteristics was not, however, significant. The response to selection was 8.4k.

Three equations were selected with matching C_p and p-values, while their RMS was smaller than that of the full equation. The three subset equations were significant at $P = 0.05$. Their responses were 6.9k, 7.1k and 7.3k. In all three equations tiller length occurred.

Apart from time of head emergence, tiller length and leaf number, the relative influence of the various variates in the multiple regression equations with Y_{DM} or Y_{DOM} as dependent characteristics agreed. Especially the effect of fresh weight of the plant was very similar in both equations. Time of head emergence and tiller length were found to

Table 43. Selection indices estimated from the parent-offspring relationship. k = selection intensity; R^2 = squared multiple correlation coefficient; G = response to selection expressed as a percentage of the mean of the parents; RMS = residual mean square.

Variates of the parent population	Traits of the aggregate breeding value											
	Y_{DM}			Y_{DOM}[1]			Y_{CL}			Y_{GS}		
	Partial regression coefficient	t-value	Relative influence	Partial regression coefficient	t-value	Relative influence	Partial regression coefficient	t-value	Relative influence	Partial regression coefficient	t-value	Relative influence
Tiller number	- 0.009	0.7	0.11	- 0.068	0.5	0.17	0.003	0.6	0.10	0.000	0.1	0.03
Time of head emergence	1.090	1.0	0.12	11.826	1.3	0.30	0.537	1.4	0.18	0.004	0.0	0.00
Tiller angle	0.985	1.6	0.14	5.718	1.1	0.19	- 0.011	0.1	0.00	0.021	0.2	0.02
Tiller length	0.288	1.5	0.18	3.065	1.7	0.44	- 0.014	0.2	0.03	- 0.018	0.6	0.08
Leaf number	- 0.018	0.1	0.01	- 2.029	1.4	0.34	0.003	0.1	0.01	0.029	1.2	0.16
Leaf width	- 0.957	0.8	0.08	- 3.045	0.3	0.06	- 0.297	0.7	0.08	0.158	0.8	0.10
Leaf length	- 0.001	0.0	0.00	- 1.294	0.3	0.05	- 0.035	0.2	0.02	0.004	0.1	0.01
Stem diameter	- 2.045	0.4	0.05	16.384	0.3	0.06	1.456	0.8	0.11	- 0.994	1.2	0.18
Tiller weight	0.051	0.1	0.02	- 0.187	0.0	0.02	- 0.126	0.7	0.15	0.031	0.4	0.09
Fresh weight of the plant	0.103	2.4	0.52	0.503	1.0	0.46	- 0.012	0.8	0.19	- 0.001	0.2	0.05
Head number	-	-	-	-	-	-	- 0.005	0.4	0.07	0.000	0.0	0.00
Y_{DM}	- 0.028	1.0	0.16	-	-	-	-	-	-	-	-	-
Y_{DOM}	-	-	-	0.127	0.2	0.07	-	-	-	-	-	-
Y_{CL}	-	-	-	-	-	-	0.079	4.6	0.48	-	-	-
Y_{GS}	-	-	-	-	-	-	-	-	-	0.081	2.3	0.29
Constant	93.817			55.198			16.328			4.235		
F-value	$F^{11}_{109} = 2.9^{**}$			$F^{11}_{38} = 1.8$			$F^{12}_{108} = 2.4^{**}$			$F^{12}_{108} = 1.2$		
R^2	0.229			0.338			0.208			0.117		
RMS	73.078			26.023			8.601			1.826		
G	5.2 k			8.4 k			6.7 k			13.2k		

** $P < 0.01$

1. based on 50 plants.

affect D_{vitro} to a large extent (Table 10) and might therefore exert a relatively large influence on Y_{DOM}, though the variation for Y_{DM} was far greater than the variation for D_{vitro} (Table 13). The change in relative influence of leaf number could not be accounted for.

Y_{CL} as a dependent characteristic The regression equation with all variates included was significant ($P < 0.01$). The largest influence on Y_{CL} of the offspring was exerted by Y_{CL}, whose contribution to the equation was significant ($P < 0.01$). The other variates contributed to a considerably smaller extent. The response of the full equation amounted to 6.7k. Only few equations occurred with matching C_p and p-values and three equations were finally selected. One equation consisted solely of Y_{CL} ($G = 5.3k$), while Y_{CL} occurred in the other two; the responses of those two equations were 5.5k and 5.6k.

Y_{GS} as a dependent characteristic The 12 variates of the full equation did not significantly contribute to the reduction of the sum of squares of Y_{GS} of the offspring. Only Y_{GS} had a significant ($P < 0.05$) t-value. The response of the full equation was 13.2k. Seven subset equations were considered for selection, but non of them showed close C_p- and p-values ($C_p < p$), while the F-values of these equations were non-significant. The response of these equations varied from 8.1k to 11.1k. Deletion of variates from the full model will therefore lead to subsets of variates with increased random error compared to the full equation, so that no subset equations were selected.

Y_{CL} and Y_{GS} showed comparable relative influences for most characteristics. The relative influence of tiller number, time of head emergence, tiller weight and fresh weight was larger in the equation with Y_{CL} as the dependent characteristic than in the one with Y_{GS}. The same had been encountered in the parent population for time of head emergence and fresh weight (Table 24), while the opposite occurred for tiller number and tiller weight. In Table 42 different responses for Y_{CL} and Y_{GS} of the various characters were presented and a similar conclusion is reached that, because of the absence of a clear correlation between Y_{CL} and % germination, the % germination is the cause of varying relative influences.

Thirty selection indices were made up with either Y_{DM}, Y_{DOM}, Y_{CL} or Y_{GS} of the offspring as the dependent characteristic and time of head emergence, fresh weight, head number, Y_{DM}, Y_{DOM}, Y_{CL} and Y_{GS} of the parent population as dependent variates in all possible combinations, depending on the definition of the aggregate breeding value.

Index values of parents and offspring from which the heritability in the narrow sense of the various indices could be estimated were calculated through the 30 equations (see Appendix 5). Indices composed of only one variate were not presented as their heritabilities in the narrow sense were equal to the ones already given in Table 40. The indices with the highest heritability, which would thus give the highest response in the yield characteristics of the offspring through selection on characters of the parent population, were those that either contained time of head emergence (Table 40), or a combination of this characteristic with fresh weight.

6.5.3 Discussion

De Wolff (1972) listed the advantages of estimating selection indices from parent-offspring relationships as follows:
- selection indices are directly estimated through multiple regression of the values of the offspring on the characteristics of the parent plants without establishing the population parameters;
- the experimental procedure is relatively simple;
- selection indices can be obtained for the selection under conditions differing from the normal cropping environment.

The latter advantage especially is thoroughly applicable to grasses as actual selection is usually carried out under spaced-plant conditions, which differ considerably from the sward conditions under which the grass will be ultimately used (see Chapter 4). However, the great danger of establishing selection indices from parent-offspring relationships through multiple regression of the yield of the offspring on the plant characteristics of the parent population, is the possibility that statistical rather than genetical relationships will rule the selection.

As selection indices with many characteristics are inapplicable, some selection procedure is required on purely statistical grounds. De Wolff (1972) applied the step-up and the step-down method of Snedecor & Cochran (1967), while in the present study a method described by Daniel & Wood (1971) was used. The method has been worked out in Appendix 2. No matter how well the selected subset of variates may fit statistically in explaining the variation of the dependent characteristic, it is its genotypic correlation with the dependent characteristic, its heritability and its practical testability that will ultimately determine the choice.

A characteristic that did emerge and which combined the above-mentioned properties to obtain a high degree of suitability for selection, was fresh weight of the plant at seed harvest. Its relative influence in the equations containing all variates with Y_{DM}, Y_{DOM} and Y_{CL} as dependent characteristics was the largest. Its heritability in the narrow sense was low (Table 40), but could be placed in Robinson's classification of heritabilities (Robinson, 1966) as medium-sized. Fresh weight displayed high phenotypic and genotypic correlations with seed yield, while its genotypic correlation with herbage yield exceeded 1 (the phenotypic correlation was high as well (Table 41). This latter correlation was caused by the large dependence between fresh weight at seed harvest and dry-matter yield at fixed periods of regrowth, so that fresh weight could hardly be regarded as an independent characteristic any longer. The fresh weight of the plant could be easily recorded in the field, with the added advantage that the open-pollinated seed could be harvested simultaneously for further testing.

In Section 6.4.3 the large location-and-error components of variance of fresh weight were discussed, while its repeatability was rather low (Table 9). The recording of fresh matter incorporated inaccuracies, leading to these effects although the correlation between the fresh weight of the plant at seed harvest and its dry-matter weight was very high (see

Section 2.2.2). Therefore, when measuring fresh weight the described disadvantages have to be taken into account by repeating the recording in time and location.

Besides the high correlation with herbage and seed yield, fresh weight showed high, positive genotypic correlations with tiller number, tiller length, tiller weight and head number (Tables 8 and 23). The fresh weight characteristic therefore comprised all these characteristics. In the regression equations each characteristic was expressed as a function of the other independent variates through a linear least-squares equation. The squared multiple correlation coefficient then expressed the linear dependence of that characteristic on the other independent characteristics. In the full equations of the four aggregate breeding values Y_{DM}, Y_{DOM}, Y_{CL} and Y_{GS} this squared multiple correlation coefficient was 0.86, 0.91, 0.87 and 0.85, respectively, thus displaying the large dependence between fresh weight and the other characteristics (data not presented).

Only the four selected subsets of variates of Y_{DM} (Appendix 4) included the characteristic of fresh weight - in the subsets of the other aggregate breeding values fresh weight was not included. The large relative influence of fresh weight in the full equation did not come to the foreground in the selected subsets and this character would therefore be omitted from the records if the selection of variates were based only on the statistical analysis as such. The importance of fresh weight was further expressed in the indices presented in Appendix 5.

(In)direct selection on herbage and seed yield also offered good perspectives (Table 42). In view of the high correlations between herbage and seed yield (Table 41) selection could be either directed to herbage or seed yield. However, the expected response to selection for seed yield was greater than that for herbage and it would therefore seem more rewarding to select for improved seed yield. Reasons for the poor response to selection for herbage yield have already been given in Sections 5.4 and 6.1. The response to selection for seed yield will be expressed in a higher number of flowering heads per unit area, leading to an increased yield of clean seed. The response in Y_{GS} is much more dependent on crop husbandry techniques acting on % germination. This latter characteristic showed a negative repeatability (Table 22), and because of the large environmental influences on this characteristic the relative influences of the independent variates could differ for Y_{CL} and Y_{GS}.

6.6 APPLICABILITY OF INDEX SELECTION IN SETARIA BREEDING

Selection indices are usually constructed to make selections on the basis of progeny means rather than for the selection of individual plants. De Wolff (1972) questioned whether with such application a selection index could sufficiently enhance the accuracy with which the genetic value of each progeny could be estimated from single or replicated plots. De Wolff (1972) advocated the use of selection indices for the selection of individuals as, by mass selection based on single plants, characteristics such as yield would give a poor estimate of the genetic value. The application of selection indices in which all information available from single plants is contained would increase the efficiency of mass selection of individual plants.

In grass breeding, initial selection is usually made from large source populations

which are very often straight introductions of natural populations. Mass selection from which high responses are anticipated, is applied, in view of the high amount of additive variance which might be present in the introduced ecotypes.

From the foregoing the application of index selection in the spaced-plant population of Nandi I appeared to be justified.

In generatively propagated grasses the paradoxical situation occurs that the ultimate utilization of the grass is made in its vegetative stage, obtained by way of a seed multiplication. Therefore both factors, herbage and seed production, are equally important in determining whether a grass variety is agronomically and economically attractive. No matter how excellently a variety performs agronomically, the economics of its seed production ultimately determine whether a variety will be commercialized.

As has been outlined in Chapters 1 and 3, seed production in cultivated tropical grasses is low compared to temperate grasses and certainly needs improvement. The ample availability of tropical grass seeds of improved varieties at reasonable prices is a prequisite in improving grassland productivity and an increased seed yield should therefore be the major breeding objective in setaria.

For intensively managed livestock farms high herbage productivity is an important characteristic of a variety, while for the less intensive farms the herbage yield distribution over the year and the persistence are important characteristics. The latter are difficult to express in figures, but the total herbage yield of the various cuts per year will be a reflection of these two characteristics. Next to seed yield, herbage yield is therefore the second breeding objective in setaria. Both characteristics were for that reason included in the aggregate breeding value.

Characteristics to be considered for inclusion in a selection index should, if possible, satisfy the following conditions:
- high genotypic correlation with the characteristics of the aggregate breeding value;
- high heritability;
- ease of recording.

Various characteristics that were thought to affect herbage yield, its quality and seed yield were included in the study of the parent population for the reasons outlined in Sections 2.2.1 and 3.3.1.

The size of the genotypic and phenotypic correlations of these characteristics with herbage and seed yield in the parent population varied (Tables 23 and 32). Tiller number, fresh weight of the plant at seed harvest and head number emerged as characteristics having the highest correlation with either herbage yield or Y_{CL}. The highest correlation with Y_{GS} was shown by fresh weight. Tiller length, leaf length and tiller weight also showed high correlations with herbage yield (Table 32), but these characteristics were contained in the fresh weight of the plant. Tiller length and tiller weight exhibited high correlations with both Y_{CL} and Y_{GS} (Table 23).

The heritabilities in the wide sense of these characteristics were high (Tables 9 and 22) and therefore met the second condition for inclusion in an index. The simplicity of recording varied from one characteristic to the other.

The stepwise elimination of the least influential variates resulted in the selection of the principal characteristics determining herbage and seed yield, that is fresh weight

of the plant and head number (Appendix 3). Both variates satisfied the requirements set for their inclusion in an index as defined earlier. The response in seed yield was approximately 1.5 times as large as that for herbage yield.

From the selection indices measured through the parent-offspring relationship (Section 6.5), fresh weight also proved to be an important characteristic affecting herbage yield and Y_{CL} as measured by its relative influence (Table 43). Another important characteristic was seed yield itself. The selection of subset equations sometimes resulted in variates being selected that were far less influential than the variates mentioned above in the full equation. These characteristics were however selected on their statistical merits rather than on their genetical relationships with the aggregate breeding value. With these indices the response of selection for seed yield was larger than that for herbage yield.

The genotypic correlation between the traits of the aggregate breeding value, herbage and seed yield, was large (Section 6.3.2 and Table 41). In Section 3.3.3 the correlation between plant size and seed yield was discussed. Large plants, that is, with a large bottom circumference because of a high tiller number and tall tillers as determined on spaced-plants, had a higher seed yield than small plants. The size of the plant also affected herbage yield, resulting in the high correlation between both characteristics.

In view of the higher response for seed yield than for herbage yield and because of the high genotypic correlation between them the aggregate breeding value should in fact consist of the seed-yield characteristic. Selection for the latter characteristic will give a correlated response in herbage yield. The composition of the index should include the variates fresh weight of the plant at seed harvest and number of heads. Time of head emergence, consistently displaying high heritability values in the various heritability calculations (Tables 9, 37, 38 and 40), should be included as a classificatory characteristic. When selection is to be carried out before flowering the index should, in addition to time of head emergence, take into account tiller number, tiller length and tiller weight. The two last-named are more cumbersome to measure than the other characteristics.

The seed yields determined on single plants were most variable (Chapter 3). When selection indices are to be established on the basis of a parent-offspring relationship, the offspring can best be evaluated for seed yield in drilled rows (if enough seed is available), while the characteristics in the parent population can be recorded from spaced plants. The seed yields of the offspring so determined can then be related to the characteristics of the parent plants.

The response obtained from the selection indices based on the phenotypic and genotypic covariances of the parent population were larger than those expected from the parent-offspring relationship. The former was based on individual plant observations, while the latter was established from individual plant observations plus progeny means. A reason for this might be the far greater variability in the parent population than in the offspring. This might have come about for the following reasons:

- the averaging of the offspring values over crop and locations whereas the parent values were only averaged over crops;
- the offspring were raised from seed after generative propagation, thus reducing variability, while the parent population originated from vegetatively collected material (which

was the original population of 4000 plants of Nandi I) by which the variability was fixed;
- the greater plant density per unit area of the offspring compared to the plant population wich might have differently affected the overground and underground competition between plants.

7 The implication of the research in a breeding programme

Some characteristics of tropical grasses in relation to temperate grasses have been discussed, the major breeding objectives for improved herbage and seed productivity in setaria have been defined, and ways have been examined of evaluating single plants. On the basis of this information, a breeding programme for setaria was established (Table 44). In principle, a similar programme could be set up for other tufted, seed propagated tropical grasses. When applied to spreading, generatively propagated grasses, single plants must be evaluated differently, as will be outlined below.

Once the grass species requiring improvement has been defined on the basis of its agronomical features, the breeding objectives, taking into account the grass' deficiencies, have been established, and the requirements mentioned in Chapter 1 have been met (i.e. the demand for improved varieties, the provision of commercial outlets to market the developed varieties and the existence of an independent agency to control seed quality), a breeding programme can be initiated.

A first step will be to make a wide collection of indigenous and exogenous ecotypes by exploration and requesting samples of existing varieties of the particular species. Ecotypes can be collected either through seed or tillers. The former has the advantages of storage and long viability of the collected material, but restricts the places of finding (when the grass is grazed, practically no inflorescences will be present), while the latter is more cumbersome, especially the problems of maintenance of the collected material during a long exploration trip, though the places of finding are not limited. When collecting tillers, most of the variability within an ecotype is fixed in the vegetative material, whereas in the case of collected seed the generative stage only reflects a part of the variability present. Seed should be harvested or tillers be taken from about 15-20 plants. Usually the breeder is more interested in as wide as possible a collection of ecotypes rather than in a large number of plants of restricted origin.

Seed of the collected tillers has to be produced for further evaluation. The collected seed has to be multiplied if the quantaties available are small. Vegetative propagules or seedlings should be raised first and each ecotype can be planted in isolation from the other in tall crops like maize or Napier grass. If there is a limit to the number of isolation possibilities, ecotypes of comparable origin can be planted in one isolation plot. At this stage some preliminary information on the time of head emergence and agronomic performance can be collected from the single plants. The collecting and bulking up of the seed of the collected material will take two to three years.

A possible narrowing of the genetical variation present within the ecotype might occur when the number of sampled plants is 15-20. If this really poses a problem and the ecotype shows promise for agricultural use, more and wider material, if still available should be collected from the places where originally found.

Table 44. A proposed breeding programme for setaria.

Duration (Years)	Phase	Characteristics to be recorded
1	Collecting indigenous and exogenous ecotypes through exploration and establishing a variety collection	
	↓	
2 - 3	Generative propagation of introductions by means of spaced plants	Time of head emergence General observations on agronomic performance
	↓	
2 - 3	Screening introductions for herbage yield in closed crop canopies, established from seed	Establishment Tiller density Persistence Disease susceptibility Drought tolerance Yield of fresh material Herbage yield distribution
	↓	
2 - 3	Study of variability within highest yielding introductions through spaced plants	Time of head emergence Fresh weight of the whole plant at seed harvest
	↓	
2 - 3	Evaluation of highest yielding plants in replicated clonal rows in a sward of another species	Time of head emergence Leafiness Evenness of heading Number of harvested heads Fresh weight at seed harvest time Y_{CL} Y_{GS} Classificatory characteristics (e.g. growth habit, leaf width, etc.)
	↓	
2	Negative mass selection in the bulked open pollinated progeny of selected clones	Generative multiplication of clonal propagules of selected plants in an isolated, randomised crossing plot
	↓	
2 - 3	Evaluation of experimental varieties in cutting and grazing trials at different locations Evaluation of experimental varieties in seed yield trials	
	↓	
	Release of the most promising variety	

Seed multiplication of the collected material brings the populations into better balance as the extremes in time of head emergence (i.e. the very early and late-heading plants) are excluded from the panmixia. To preserve the variability of promising ecotypes, as has been observed in the seed multiplication plots, the plants of such ecotypes

can be maintained by clonal propagation.

The amount of seed to be produced has to suffice for the establishment of a herbage-yield trial consisting of plots sown in rows or broadcast, to determine the agronomic promise, if any, of the collected material and introduced varieties compared to existing varieties. The entries should be grouped according to their time of head emergence, as observed in the seed multiplication plots, and should be replicated at least twice. If not enough seed is available, the introductions can be evaluated in blocks of a fixed size which include two or three standard varieties replicated throughout the trial field.

Herbage yield determinations by cutting should be carried out at regular intervals according to the maturity of the various groups of introductions. As this first screening aims only at distinguishing between promising and poor introductions determination of fresh weight alone (without dry-matter determinations) will suffice for the purpose.

Other things that have to be observed are:

- establishment after sowing (dependent on seed quality);
- tiller density;
- persistency;
- susceptibility to diseases;
- drought tolerance.

In addition to the total yield of fresh material, distribution of the yield is an important characteristic. This stage of the breeding programme should take at least two years. The longer the screening period, the more interesting will the differences be that show up between introductions, depending on the quality of the collected material.

Promising introductions as regards herbage yield, yield distribution and the other characteristics mentioned can be multiplied directly for commercial use. But even though the general appearance of the ecotype or the introduced variety may seem uniform, considerable variation may still exist within the latter and lead to a genetic shift during seed multiplication so that the variety will turn out to be unstable. If breeders' rights are established (the Kenyan government is in fact contemplating the introduction of plant breeders' rights), the variety will not be protected because of lack of uniformity. Moreover, at this stage of the breeding programme little is known about the seed-yielding ability of the promising introduction, which will be adversely affected by heterogeneity.

The next step will therefore be to study the variability within the introductions by means of single plants at wide spacing. Only those introductions that emerged as the most promising for the before-mentioned characteristics are evaluated. This can be done on plants raised from the bulked seed of the introductions or on plants taken out of the rows or the swards of the herbage-yield screening trial. The advantage of the last-named may be that a shift has occurred towards herbage productivity under the cutting management applied.

It was concluded in Section 4.4 that spaced plant fields were an appropriate means of assessing the variability within a population and grouping plants according to observed characterictics. At this stage of the breeding programme when large numbers of plants have to be screened the evaluation of plants at wide spacing is justified, though it should be emphasized that, in view of the results discussed in Chapter 4, the plants selected under these conditions will not necessarily be similar to those selected under mo-

re competitive stress.

In the case of spreading species, single plants can be evaluated in little swards of their own, separated from each other by another, tufted species or by soil cultivation and herbicides.

Time of head emergence and fresh weight of the plant at seed harvest are the two most important characteristics to be recorded in the spaced-plant population. Time of head emergence is the first criterion for grouping the plants accordingly. Matching data of heading is the main requisite for obtaining uniformity. The repeatability of this characteristic was low, however (Tabel 9), partly because of the absence of a clear photoperiodic response as discussed in Chapter 1. Differences for the same plant from season to season can therefore be expected. The fresh weight of the plant at seed harvest proved to be the characteristic most important in determining herbage and seed productivity (Chapters 2, 3 and 6), which justifies recording it by cutting and weighing the whole plant in situ. The low repeatability of fresh weight (Table 9) and the high degree of susceptibility to the environmental variance, necessitate recording this characteristic for at least two crops.

It should be realised that the correlation between herbage and seed yield was observed at 1^{o} North latitude, where differences in daylength were practically nil during the year. Recording the fresh weight of the plant at places farther from the equator, where greater differences in daylength may cause a photoperiodic response by the grass, may therefore not have so predictive a value of both herbage and seed yield in a positive sense.

From the large spaced-plant population the plants highest in fresh weight at seed harvest are selected for further evaluation in clonal rows, preferably replicated in a sward of another species (Chapter 4). In view of the size of the coefficients of rank correlation presented in Chapter 4, part of the plants that excelled under wide spacing will fail under the more intensive competition of the accompanying grass.

In the first screening trial, selection was directed towards herbage yield, distribution and other favourable agronomical characteristics, while in the spaced-plant population selection was directed towards both herbage and seed yield through the fresh-weight characteristic as discussed in Section 6.6. The effectiveness of recording Y_{CL} (and thus Y_{GS}) on the spaced-plants is low in view of the high coefficient of variation for Y_{GS} on single plants (Table 22) and its determination is, moreover, very labour intensive. The narrowed population present in clonal rows offers a better opportunity for refined observations on the seed-yielding ability of the selected plants. For spreading species, evaluation of the selected plants can be repeated in swards of their own.

The characteristics that should be recorded in different crops are:

- time of head emergence;
- leafiness;
- evenness of heading within plants (rows);
- number of harvested heads;
- fresh weight per row at seed harvest;
- Y_{CL};
- Y_{GS}.

In view of the positive, significant correlation between D_{vitro} and % leaf (Table 14) selection for leafiness is thought to affect the nutritive value positively. Evenness of heading within plants will contribute to the synchronization of flowering (see Section 3.1). Head number was the most important characteristic of the three components determined (Table 21). In addition to Y_{CL}, Y_{GS} has to be determined in view of the low correlation between Y_{CL} and % GS (see Table 20 and Section 3.3.3). The three last-named characteristics can only be determined after flowering. Tiller number, tiller length and tiller weight showed high genotypic correlations with Y_{CL} and Y_{GS} (Table 23) and selection for these characteristics, which displayed high genotypic correlation coefficients with fresh weight of the plant at seed harvest (Table 8), makes indirect selection for Y_{CL} and Y_{GS} possible before flowering. These characteristics are more laborious to measure, however.

The characteristics mentioned can be included in selection indices estimated from the replication of the clonal rows according to the method described in Section 6.3. The aggregate breeding value should consist only of Y_{CL} or Y_{GS} as was concluded in Section 6.6.

Though the seed yield determination for clonal rows will be more accurate than for single plants, seed yield should be determined for at least two crops in view of the considerable season-to-season differences which were also observed in closed crops (Boonman, 1972a).

At this stage, characteristics such as growth habit, leaf width, plant height, leaf colour and panicle colour can be assessed for plant grouping directed towards these properties in the next step of the breeding programme. These characteristics are thus merely classificatory.

The next step will be the composition of various synthetic varieties, for which two approaches can be envisaged.

One is to put together seed of the highest seed-yielding clones harvested from the clonal rows and selected before or after flowering, ensuring the closest possible resemblance to each other of the constituting clones. From the bulked seed, plants are raised and planted at wide spacing for negative mass selection - plants deviating in appearance from the population mean are removed before flowering. Variation in the population, consisting of progenies of plants selected from the clonal rows before flowering, will be less than that of the population consisting of plants selected after flowering. The seed harvested from the plants remaining after the negative mass selection will be the ultimate variety.

The other approach is to plant clonal propagules of the highest seed-yielding and phenotypically matching plants in a randomized, isolated crossing plot to produce the variety. This method aimes at panmixia of the selected plants, all plants being assumed to be fertilized by the same homogeneous pollen cloud, while with the use of seed harvested from the clonal rows the neighbour effect on fertilization plays an important role. A refinement on the method of randomized, isolated crossing plots, the 'polycross', is to test the progenies of the individual harvested plants, whereupon the parent clones that will ultimately form the basis of the variety, can be selected on the basis of the performance of the half-sib families. The progeny testing should preferably be done in

swards. The herbage and/or seed yields can be related to the characteristics of the parent plants for the composition of selection indices as presented in Section 6.5. Genotypes with a good general combining ability are selected by this method. The progeny testing however, lengthens the time required for the breeding programme and is for that reason not often carried out in practice.

From the results discussed in Section 2.3 and Chapter 6 it can be anticipated that the plants selected as combining both high herbage and high seed yield will be characterized by a high tiller number, erect to semi-erect growth habit, early time of head emergence, heavy and tall tillers and large number of flowering heads. However, late-heading plants that combine these characteristics occur as well but at a much lower frequency. The long tiller length and the heavy tiller weight will adversely affect D_{vitro} (Table 8), but in view of the slight variation for D_{vitro} (Table 13) at a given period of regrowth, the resulting product of D_{vitro} and Y_{DM}, Y_{DOM}, will be largely determined by Y_{DM}.

In a final evaluation trial for herbage yield the various experimental varieties should be compared with known standard varieties in cutting and grazing trials, preferably at different locations. The seed-yielding ability has to be assessed in separate trials in an environment appropriate for seed production. Once an experimental variety has been shown to be an improvement on existing varieties, the experimental variety should be released commercially.

It should be realised that the greater part of the material originally collected has been rejected at earlier stages of the programme and that only a small part is left for intensive evaluation.

The broader the base population subjected to the first herbage-yield screening trial, the greater the chances of finding interesting material for further evaluation. However, this depends very much on the available time, labour and financial means. But, independently of the size of the source population, it can be stated as a general rule that, at each step of the breeding programme, 10% is selected.

Summary

The major shortcomings of cultivated, generatively propagated tropical grasses compared to temperate grasses, are their poor nutritive value and the low seed yields. The present study on a tropical grass was set up to gain more insight into the plant characteristics which determine herbage yield and its quality (as expressed by in vitro digestibility) and seed yield. With this information the phenotypic characteristics upon which selection should be based were defined in relation to their inheritance as estimated from clonal replication, a half-sib relationship and a parent-offspring relationship.

Chapter 1 deals with the early exploratory work on ecotypes and varieties carried out at the Grassland Research Station in Kitale, Kenya during the fifties. *Setaria sphacelata* (Schumach.) Stapf and Hubbard ex Moss (setaria) emerged as a productive species, of which the Nandi ecotype was the most promising. The development, between 1954 and 1956, of two varieties out of this ecotype is outlined. Owing to the absence of a clear photoperiodic response, tropical grasses undergo continuous stem elongation. Breeding was therefore directed towards late head emergence and leafiness. After the commercial release of the two late-heading varieties it was found that these two varieties brought no improvement in herbage yield compared to the original Nandi ecotype from which they were bred. Seed yield in particular was considerably reduced. A new breeding programme was therefore initiated in 1971, of which this study formed an integral part.

The relationship between in vitro digestibility and dry-matter yield and various plant characteristics is dealt with in Chapter 2. Out of a spaced-plant population of 4000 plants of the Nandi ecotype (after the release of the two late-flowering varieties subsequently called Nandi I) 121 plants were chosen at random. In vitro digestibility and various plant characteristics of the 121 spaced-plants were measured on tillers at a similar growth stage. When so compared, tillers of early-heading plants had a higher digestibility than late-heading plants.

Highly digestible tillers were further characterized by short length, narrow leaves and light weight, which affected dry-matter yield adversely. Selecting plants with a high tiller number would compensate this loss in herbage yield. The correlation between digestibility and dry-matter yield was negative when the whole plants were compared at three, six and nine weeks of regrowth. A wide variation for digestibility and dry-matter yield was observed at each regrowth period, which allowed the selection of plants combining a high expression for both characteristics. However, the increase achieved in the ultimate product of digestibility and dry-matter yield, that is the yield of digestible organic matter, was largely due to an increase in dry-matter yield rather than to improved digestibility. It would therefore appear to be more rewarding to select for the first-named characteristic than for the latter. The large observed range in digestibility values of the spaced plants was not found in an experiment with eight experimental

varieties of varying maturity, broadcast in swards and cut during undisturbed regrowth of varying age. It was concluded that the prospects for selection for digestibility in panmictic species are not bright, because the initially observed differences in digestibility, as observed on spaced plants, cannot be repeated under sward conditions, due to a plant × environment interaction. Apomictic or vegetatively propagated, spreading species are much more promising.

In Chapter 3 the seed yield and three seed components were measured and related to the plant characteristics determined in Chapter 2. Of the three components head number, head length and 1000-grain weight, the first proved to be the most important as a determinant of seed yield. The clean seed evinced a low and varying viability, which was expressed by the very low correlation between clean seed yield and % germination. Plants with a high yield of clean seed were early-heading and large in size. Compared with low-seed-yielding plants, the former had more and taller flowering heads with smaller grains.

Initial selection in grasses is usually based on the performance of single, widely spaced plants. Selection is thus made under conditions which differ from the sward conditions under which the variety will ultimately be used. In order to surmount this difficulty the 121 setaria plants were also evaluated in a sward of another species and their performance was compared with that in monoculture as described in Chapter 4. In view of the size of the rank-correlation coefficients of various characteristics it was concluded that testing at wide spacing in monoculture and mixed culture gave different results, but that testing in monoculture is still justified at the initial stages of a breeding programme.

In the experiment, described in Chapter 5, plants with an erect, lax and prostrate growth habit, respectively were compared in monoculture and in mixed culture at two cutting frequencies. The erect-growing plant type was found to be the most productive in dry-matter yield and to have the highest competitive ability under this particular management.

In Chapter 6 the simultaneous selection was worked out for both herbage and seed yield by means of selection indices. Selection indices were obtained from the phenotypic and genotypic (co)variances estimated from the clonal replication of the 121 plants and from the parent-offspring relationship of these plants. In the first-mentioned selection indices, fresh weight of the plant at seed harvest proved to be the most important characteristic determining herbage and seed yield. Head number was an additional important characteristic affecting dry-matter and clean-seed yields. In the full equation of the parent-offspring relationship, as estimated from the multiple regression of the offspring yield on the characteristics of the parent population, fresh weight at seed harvest exerted the largest influence on herbage yield, whereas the greatest influence on seed yield was exerted in fact by seed yield itself. The conclusion was that, in view of the high genotypic correlation between herbage and seed yield and the higher selection response expected from seed yield, selection should only be directed towards improved seed yield, especially of clean seed. An increase in the yield of germinating seeds will, in addition to a high clean-seed yield, depend on the application of correct husbandry techniques.

The index should be built up out of time of head emergence and fresh weight of the plant at seed harvest, when selection is carried out after flowering. If selection is made before flowering, tiller number, tiller length and tiller weight as found at a compa-

rable growth stage should be included.
Finally, a breeding programme for setaria is suggested in which the major findings of the present study are incorporated (Chapter 7). After initial screening for agronomic performance of the ecotypes and varieties introduced, selection is directed towards the improvement of the seed-yielding ability.

Samenvatting

Generatief vermeerderde grassoorten uit tropische streken vertonen een lagere voedingswaarde en lagere zaadopbrengsten dan grassoorten uit gematigde streken. In dit onderzoek werd een tropische grassoort onderzocht op kenmerken die de grasopbrengst en haar kwaliteit (zoals bepaald door de verteerbaarheid in vitro) en zaadopbrengst bepalen. Met deze informatie konden de fenotypische kenmerken waarop selectie zich zou moeten richten, worden gekozen. Bij deze keuze werd rekening gehouden met de vererving van die kenmerken. De erfelijkheidsgraad werd geschat aan de hand van klonen, half-sibs en ouder-nakomelingschap relaties.

In hoofdstuk 1 wordt beschreven hoe in de vijftiger jaren rassen en in de natuur verzameld materiaal (ecotypen) werden geëvalueerd op het Grassland Research Station in Kitale, Kenya. *Setaria sphacelata* (Schumach.) Stapf and Hubbard ex Moss (setaria) bleek een produktieve soort te zijn met het Nandi-ecotype als meest belovende in grasopbrengst. Tussen 1954 en 1965 werden twee rassen uit dit ecotype ontwikkeld. Bij grassen uit tropische streken vindt stengelstrekking gedurende het gehele groeiseizoen plaats door de afwezigheid van een duidelijke daglengtereactie. De veredeling richtte zich daarom op planten die laat doorschoten en zeer bladrijk waren. Nadat deze twee rassen, die laat doorschoten, op de markt waren gebracht, bleek dat deze rassen geen grotere grasopbrengst dan het originele Nandi-ecotype hadden. Speciaal de zaadopbrengst was aanzienlijk gereduceerd. In 1971 werd daarom een nieuw veredelingsprogramma opgezet, waarvan dit onderzoek een integraal deel vormde.

In hoofdstuk 2 worden de relaties tussen verteerbaarheid in vitro, drogestofopbrengst en verscheidene plantkenmerken beschreven. Uit een veld met 4000 afzondelijke planten van het Nandi-ecotype (na het op de markt brengen van de twee laat doorschietende rassen Nandi I genoemd) werden willekeurig 121 planten gekozen. Van deze planten werden verscheidene kenmerken gemeten en van spruiten die in een gelijk groeistadium verkeerden, werd de verteerbaarheid in vitro bepaald. Spruiten van vroeg doorschietende planten, vergeleken in hetzelfde groeistadium, hadden een hogere verteerbaarheid dan spruiten van laat doorschietende planten. Hoog verteerbare spruiten werden verder gekenmerkt door een korte lengte, smalle bladeren en weinig gewicht, wat de drogestofopbrengst negatief beïnvloedde. Door planten met een hoog spruitaantal te selecteren, kan dit verlies in grasopbrengst gecompenseerd worden. Wanneer de gehele planten vergeleken werden bij respectievelijk 3, 6 en 9 weken hergroei, bestond een negatieve correlatie tussen verteerbaarheid en drogestofopbrengst. Bij elke hergroeiperiode werd een grote variatie in verteerbaarheid en drogestofopbrengst waargenomen, waardoor het mogelijk was planten te selecteren die hoge waarden vertoonden voor beide kenmerken. De verkregen toename in het produkt van verteerbaarheid en drogestofopbrengst, de opbrengst aan verteerbare organische stof, werd grotendeels veroorzaakt door een verhoogde drogestofopbrengst en niet door

een verbeterde verteerbaarheid. Het is daarom aan te raden om op drogestofopbrengst te selecteren. De grote verschillen in verteerbaarheid bij de afzonderlijke planten werden niet gevonden in een proef met acht experimentele rassen in een gesloten zode. Deze rassen waren van verschillende vroegheid, breedwerpig gezaaid en geoogst bij ongestoorde hergroei van verschillende ouderdom. De conclusie was dat de vooruitzichten voor het selecteren op verteerbaarheid in kruisbevruchtende soorten niet gunstig zijn aangezien de eerst waargenomen verschillen aan afzonderlijke planten niet onder zode-omstandigheden herhaald kunnen worden ten gevolge van een plant × milieu interactie. Uitloper vormende grassen die zich apomictisch of vegatatief vermeerderen bieden meer perspectief voor selectie.

In hoofdstuk 3 worden de metingen van de zaadopbrengst en drie zaadcomponenten aan de 121 planten beschreven. Zaadopbrengst en -componenten werden gerelateerd aan de plantkenmerken uit hoofdstuk 2. Van de drie zaadcomponenten aaraantal, aarlengte en 1000-korrelgewicht, was aaraantal het meest belangrijk voor het bepalen van de zaadopbrengst. Het geschoonde zaad had een lage en variabele kiemkracht, hetgeen tot uitdrukking kwam in de lage correlatie tussen geschoond zaad en kiempercentage. Planten met een hoge opbrengst aan schoon zaad waren vroeg doorschietend en fors van grootte. In vergelijking met planten met een lage zaadopbrengst, bezaten planten met een hoge zaadopbrengst meer en langere bloeiwijzen met kleinere zaden.

De eerste selectie in grassen wordt meestal gemaakt op basis van de prestatie van afzonderlijke planten, geplant op ruime afstand. Deze selectie wordt dus uitgevoerd onder omstandigheden die afwijken van de zodeomstandigheden waaronder het ras uiteindelijk gebruikt zal worden. Om niet aan dit probleem voorbij te gaan zijn de 121 setaria planten ook geëvalueerd in een zode van een andere soort en hun prestatie werd vergeleken met die in monocultuur. Dit is beschreven in hoofdstuk 4. De rangcorrelatiecoëfficiënten van verscheidene kenmerken toonden aan dat het toetsen in ruime stand in moncultuur en het toetsen in gemengde cultuur verschillende resultaten opleverde, maar dat het toetsen in monocultuur gerechtvaardigd is aan het begin van een veredelingsprogramma.

In hoofdstuk 5 wordt een proef beschreven, waarin de grasopbrengst van planten met een rechtopgaande, een wijd uitstaande en een platte groeiwijze in monocultuur en mengsels bij twee maaifrequenties worden vergeleken. De planten met een rechtopgaande groeiwijze bleken het meest produktief in drogestofopbrengst en hadden onder de in de proef heersende omstandigheden de grootste concurrentiekracht.

In hoofdstuk 6 is de gelijktijdige selectie op gras- en zaadopbrengst door middel van selectie-indices uitgewerkt. Selectie-indices werden verkregen via de fenotypische en genotypische (co)varianties van klonen van de 121 planten en via de ouder-nakomelingschapsrelatie van de 121 planten. Bij de selectie-indices geschat uit de klonen was het vers gewicht van de plant op het tijdstip van de zaadoogst het belangrijkste kenmerk voor de drogestof- en zaadopbrengst. Het aaraantal was eveneens een belangrijk kenmerk voor de drogestof- en zaadopbrengst. In de vergelijking van de ouder-nakomelingschapsrelatie, zoals geschat uit de multiple regressie van de opbrengst van de nakomelingen op de kenmerken van de ouderpopulatie, oefende het vers gewicht van de plant op het tijdstip van zaadoogst de grootste invloed uit op de zaadopbrengst, terwijl de grootste invloed op zaadopbrengst werd uitgeoefend door de zaadopbrengst zelf. Gezien de sterke ge-

notypische correlatie tussen gras- en zaadopbrengst en de grotere selectieresponse van de zaadopbrengst, moet de selectie zich alleen op de zaadopbrengst richten, in het bijzonder op de opbrengst aan geschoond zaad. Een verhoging in opbrengst aan kiemend zaad hangt, naast een hoge opbrengst aan schoon zaad, af van toepassing van de juiste teelttechnieken. De selectieindex moet worden samengesteld uit de kenmerken tijdstip van doorschieten en vers gewicht van de plant op het tijdstip van de zaadopbrengst, wanneer selectie na de bloei wordt toegepast. Wanneer voor de bloei geselecteerd wordt, dan dienen spruitaantal, spruitlengte en spruitgewicht, gemeten in een vergelijkbaar groeistadium, opgenomen te worden.

Tenslotte wordt in hoofdstuk 7 een veredelingsprogramma voor setaria voorgesteld, waarin de belangrijkste resultaten van deze studie zijn verwerkt. Na onderzoek naar de teeltkundige eigenschappen van de geïntroduceerde ecotypen en rassen, wordt de selectie gericht op de verbetering van het zaadopbrengend vermogen.

APPENDIX I. METHODS USED AND DEFINITIONS OF CHARACTERISTICS

When planting vegetative material or sowing, single super phosphate was applied to the soil at a rate of 40 kg of phosphate per hectare. The experiments were top-dressed with ammonium sulphate nitrate (ASN) containing 26% nitrogen.

The following characteristics were measured on spaced plants:
- Tiller number: the number of tillers per tuft, three weeks after the cleaning cut;
- IHE = Time of initial head emergence: scored on a weekly basis when more than 10 heads had fully emerged; 1 being the first week in which the first plant(s) showed more than 10 heads;
- Tiller angle: expressed as the ratio between the circumference at the height of the flag leaf and at the base of the plant at IHE.

At IHE the following characteristics of spaced plants were measured on tillers, when the tip of the emerging head was just visible above the subtending leaf sheath:
- Tiller length: the distance between the base of the tiller, cut at 15 cm above the ground level, and the ligule of the flag leaf (cm);
- Leaf number: the number of leaves, including dead ones;
- Leaf width: the width of the second leaf under the flag leaf at its widest part (cm);
- Leaf length: the length of the second leaf under the flag leaf as measured from the ligule to the tip of the leaf in extended position (cm);
- Stem diameter: the diameter of the stem at the height of the second leaf under the flag leaf (mm);
- Tiller weight: fresh tillers were dried in a forced draught oven at 100 ^{o}C and weighed (g).

Dry-matter percentages of spaced plants or closed crop canopies were determined from 500-g samples of fresh material, which were dried in a forced draught oven at 100 ^{o}C and weighed.
- Y_{DM} = Yield of dry matter: the product of dry-matter content and the yield of fresh material.

Leaf-blade and stem (including leaf sheaths) separations at the ligule were made by hand on 250-g samples of fresh material. The components were dried in a forced draught oven at 100 ^{o}C and weighed.
Dried samples of fresh material were ground and passed through a 1-mm screen.
- D_{vitro} = % digestible organic matter of the dry matter: in vitro digestibility was

determined in duplicate according to the method of Tilley and Terry (1963). Standard samples of known in vitro digestibility were analysed concurrently.

At seed harvest (about seven weeks after IHE) the panicles were cut and stored in paper bags. Observations were taken as follows:
- Fresh weight of the plant: the whole plant was cut at a height of 15 cm and weighed at time of seed harvesting (dry-matter percentage was not determined).
- Number of heads
- Head length of 25 heads
- 1000-grain weight, determined in duplicate
- Y_{CL} = yield of clean seed: seed was threshed out by hand, cleaned on a "Brabant" clipper and weighed.
- % GS = germination percentage: 200 seeds of the clean seed were germinated in duplicate as described by Boonman (1972b).
- Y_{GS} = yield of germinating seeds: the product of % GS and Y_{CL}.

The terms % PGS and Y_{PGS} encountered in the literature have the following meanings:
- % PGS = pure germinating seeds: the product of % purity and % GS.
- Y_{PGS} = yield of pure germinating seeds: the product of % purity, % GS and Y_{CL}.

APPENDIX 2. THE SELECTION OF INDEPENDENT VARIABLES AS THE BEST PREDICTORS OF A DEPENDENT VARIABLE

Introduction

The method of stepwise multiple regression of Snedecor & Cochran (1967) has been widely used to determine the variables which contribute most to the explanation of the total variance of a dependent variable. The main shortcoming of this method is that only one equation is selected as the best predictor, whereas in fact, when the independent variables are mutually correlated, stepwise regression may ignore combinations of variables wit a better fit than the one selected. Moreover, backward and forward selection may lead to different results.

Daniel & Wood (1971) discuss a computer program, the Linear Least-Squares Curve-Fitting Program, which enables the user to select several subsets of variables that fit the data as optimally as the full equation, containing all variables.

Linear Least-Squares Curve-Fitting Program

A dependent variable y may be explained through k independent variables x, by fitting the data to a linear equation of the following model:

$$y_j = \beta_o + \beta_1 x_{j1} + \beta_2 x_{j2} + \cdots \beta_i x_{ji} + \cdots \beta_k x_{jk} + e_j$$

in which

y_j = the observation of the dependent variable y on the j^{th} individual y
β_o = the intercept of the equation
β_i = the partial regression coefficient of the i^{th} independent variable x
x_{ji} = the observation of the i^{th} independent variable x on the j^{th} individual
e_j = random error of the j^{th} observed value of the independent variables x
j = 1, 2, ..., N.

The random error e_j has the following properties:
- expected value of e_j is zero;
- variance of e_j is $\sigma^2(y)$, which remains constant for all values of x_i and true observations of y;
- e_j are uncorrelated.

The coefficients of the equation are found by minimizing the sum of squares of the differences between each observed value y_j and its corresponding fitted value Y_j.

The selection of equations with a smaller number of independent variables than the full equation, approaching the fit of the data to the equation with all variables included optimally, is carried out by a statistic called C_p which is defined as

$$C_p = \frac{RSS_p}{s^2} - (N-2p)$$

in which

RSS_p = residual sum of squares in subset equation,
s^2 = residual mean square in full equation,
N = number of observations, and
p = number of parameters in the subset equation. In the full equation p = k if $b_o = 0$, in which b_o is an estimation of β_o. If b_o is present : p = k + 1

The residual sum of squares from an equation contains both bias error, due to lack of fit, and random error. The C_p value of a p-term equation estimates the ratio of the sum of squared biases in y at all N data points over the variance of random error.
In the selection procedure for a subset of variables the C_p values of a number of subset equations are plotted against p. Those equations with low bias will be close to the line $C_p = p$. Bias can be reduced by adding appropriate variables to the model (for the equation that contains all variables $C_p = p$), but the total prediction variance will consequently increase. Therefore only those equations that contain a small number of parameters and whose C_p values are close to p are candidates for selection, provided they are the most suitable in a practical sense

The C_p search starts with a comparison of C_p values of the variables by successively including them in equations in descending order of their corresponding t-values. All variables that contribute to a minimum C_p value of a certain equation, excluding the last two added, constitute the "basic set".
A search is then carried out among combinations of the remaining variables, including the basic set in any case. If k > 12, this search may be of a factorial type, excluding

the variables of the basic set.

To test the validity of the full model the standard deviation is calculated from observations which are near neighbours in the predictor space. This value is compared with the standard error from the best-fitting equation. If these values agree there is no evidence of lack of fit.

The relative influence of the i^{th} independent variable in an equation is calculated as follows:

$$\text{relative influence} = \frac{|b_i| w_i}{w_y}$$

in which

b_i = the partial regression coefficient of the i^{th} independent variable x

w_i = the range of the i^{th} independent variable x

w_y = the range of the dependent variable y

The relative influence describes the fraction of the total change in the dependent variable that can be accounted for by the accompanying total change in the i^{th} independent variable.

APPENDIX 3. SELECTION INDICES FOR THE SIMULTANEOUS SELECTION ON HERBAGE AND SEED YIELD
THE UNDERLINED VARIATE IS THE LEAST INFLUENTIAL OF EACH EQUATION AND WILL BE ELIMINATED IN THE NEXT STEP.

Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$Y_{DM} + 5Y_{CL}$	Tiller number	0.2265	0.8403	39.8820	56.3919	0.7072	20.2k	31.5k
	Time of head emergence	0.9319	0.1940					
	Tiller angle	0.5491	0.2385					
	Tiller length	0.3796	1.0838					
	Leaf number	-0.4076	2.7295					
	Leaf width	0.2147	0.7648					
	Stem diameter	0.7370	0.3665					
	Tiller weight	0.7122	0.7275					
	Fresh weight	0.0764	2.2336					
	Head number	0.1296	4.0139					
$Y_{DM} + 5Y_{CL}$	Tiller number	0.2375	0.9376	39.8047	56.3919	0.7059	20.1k	31.5k
	Tiller angle	0.6373	0.3332					
	Tiller length	0.3615	0.9988					
	Leaf number	-0.4046	2.7015					
	Leaf width	0.2137	0.7604					
	Stem diameter	0.5768	0.2473					
	Tiller weight	0.8616	1.2834					
	Fresh weight	0.0701	2.0444					
	Head number	0.1210	3.8538					
$Y_{DM} + 5Y_{CL}$	Tiller number	0.2280	0.8736	39.7062	56.3919	0.7041	20.0k	31.4k
	Tiller angle	0.6362	0.3337					
	Tiller length	0.3624	1.0088					
	Leaf number	-0.4068	2.7461					
	Leaf width	0.2459	1.0897					
	Tiller weight	0.9417	1.6156					
	Fresh weight	0.0719	2.1766					
	Head number	0.1167	3.6699					

APPENDIX 3. SELECTION INDICES FOR THE SIMULTANEOUS SELECTION ON HERBAGE AND SEED YIELD THE UNDERLINED VARIATE IS THE LEAST INFLUENTIAL OF EACH EQUATION AND WILL BE ELIMINATED IN THE NEXT STEP - CONTINUED

Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$Y_{DM} + 5Y_{CL}$	Tiller number	0.2213	0.8300	39.5737	56.3919	0.7018	19.9k	31.3k
	Tiller length	0.3230	0.8359					
	Leaf number	-0.4063	2.7576					
	Leaf width	0.2495	1.1307					
	Tiller weight	0.9838	1.7940					
	Fresh weight	0.0705	2.1098					
	Head number	0.1160	3.6537					
$Y_{DM} + 5Y_{CL}$	Tiller length	0.3044	0.7572	39.2453	56.3919	0.6959	19.5k	31.0k
	Leaf number	-0.3536	2.2419					
	Leaf width	0.2427	1.0889					
	Tiller weight	0.9141	1.5903					
	Fresh weight	0.0880	4.0091					
	Head number	0.1373	6.1752					
$Y_{DM} + 5Y_{CL}$	Leaf number	-0.3416	2.1311	38.9481	56.3919	0.6907	19.4k	30.8k
	Leaf width	0.2078	0.8339					
	Tiller weight	1.2848	4.9463					
	Fresh weight	0.0890	4.1670					
	Head number	0.1508	8.2690					
$Y_{DM} + 5Y_{CL}$	Leaf number	-0.3789	2.7582	38.6233	56.3919	0.6849	19.4k	30.5k
	Tiller weight	1.5003	8.3416					
	Fresh weight	0.0941	4.8300					
	Head number	0.1447	7.8458					
$Y_{DM} + 5Y_{CL}$	Tiller weight	1.1706	6.1892	37.5580	56.3919	0.6660	19.6k	29.6k
	Fresh weight	0.0898	4.6684					
	Head number	0.1463	8.5207					
$Y_{DM} + 5Y_{CL}$	Tiller weight	1.6866	20.5076	35.8047	56.3919	0.6349	18.1k	28.3k
	Head number	0.2159	41.4150					
$Y_{DM} + 5Y_{CL}$	Head number	0.2117	100.0000	28.4620	56.3919	0.5047	12.3k	22.8k
$Y_{DM} + Y_{CL}$	Tiller number	0.1801	1.0711	28.1044	37.2044	0.7554	20.6k	31.3k
	Time of head emergence	0.7505	0.2535					
	Tiller angle	0.4778	0.3639					
	Tiller length	0.2690	1.0962					
	Leaf number	-0.2474	2.0175					
	Leaf width	0.1253	0.5238					
	Stem diameter	0.5659	0.4353					
	Tiller weight	0.5229	0.7901					
	Fresh weight	0.0588	2.6731					
	Head number	0.0795	3.0279					
$Y_{DM} + Y_{CL}$	Tiller number	0.1890	1.1981	28.0332	37.2044	0.7535	20.5k	31.3k
	Tiller angle	0.5489	0.4988					
	Tiller length	0.2544	0.9976					
	Leaf number	-0.2450	1.9895					
	Leaf width	0.1245	0.5195					
	Stem diameter	0.4369	0.2861					
	Tiller weight	0.6432	1.4434					
	Fresh weight	0.0537	2.4288					
	Head number	0.0726	2.7817					

APPENDIX 3. SELECTION INDICES FOR THE SIMULTANEOUS SELECTION ON HERBAGE AND SEED YIELD THE UNDERLINED VARIATE IS THE LEAST INFLUENTIAL OF EACH EQUATION AND WILL BE ELIMINATED IN THE NEXT STEP - CONTINUED

Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$Y_{DM} + Y_{CL}$	Tiller number	0.1818	1.1215	27.9530	37.2044	0.7513	20.4k	31.2k
	Tiller angle	0.5481	0.5001					
	Tiller length	0.2551	1.0088					
	Leaf number	-0.2467	2.0293					
	Leaf width	0.1489	0.8046					
	Tiller weight	0.7039	1.8233					
	Fresh weight	0.0551	2.5865					
	Head number	0.0693	2.5999					
$Y_{DM} + Y_{CL}$	Tiller number	0.1760	1.0639	27.8132	37.2044	0.7476	20.2k	31.2k
	Tiller length	0.2212	0.7934					
	Leaf number	-0.2462	2.0425					
	Leaf width	0.1520	0.8481					
	Tiller weight	0.7402	2.0587					
	Fresh weight	0.0539	2.5027					
	Head number	0.0688	2.5838					
$Y_{DM} + Y_{CL}$	Tiller number	0.1672	0.9786	27.5925	37.2044	0.7416	20.1k	30.9k
	Leaf number	-0.2355	1.9061					
	Leaf width	0.1264	0.6140					
	Tiller weight	1.0059	5.8986					
	Fresh weight	0.0553	2.6850					
	Head number	0.0794	3.8083					
$Y_{DM} + Y_{CL}$	Tiller number	0.1643	0.9568	27.4231	37.2044	0.7371	20.1k	30.6k
	Leaf number	-0.2575	2.3766					
	Tiller weight	1.1375	9.1699					
	Fresh weight	0.0586	3.1108					
	Head number	0.0759	3.5639					
$Y_{DM} + Y_{CL}$	Leaf number	-0.2182	1.8413	27.1608	37.2044	0.7300	19.7k	30.4k
	Tiller weight	1.0635	8.4831					
	Fresh weight	0.0715	5.6677					
	Head number	0.0912	6.2543					
$Y_{DM} + Y_{CL}$	Tiller weight	0.8737	6.8660	26.6606	37.2044	0.7166	19.8k	29.5k
	Fresh weight	0.0691	5.5004					
	Head number	0.0922	6.6429					
$Y_{DM} + Y_{CL}$	Tiller weight	1.2704	23.9604	25.1942	37.2044	0.6772	18.3k	28.2k
	Head number	0.1457	37.0517					
$Y_{DM} + Y_{CL}$	Head number	0.1425	100.0000	19.1576	37.2044	0.5149	12.3k	22.8k
$5Y_{DM} + Y_{CL}$	Tiller number	0.2057	1.4252	27.8568	35.4156	0.7866	20.9k	30.8k
	Time of head emergence	0.8694	0.3463					
	Tiller angle	0.5977	0.5802					
	Tiller length	0.2661	1.0913					
	Leaf number	-0.1862	1.1575					
	Leaf width	0.0860	0.2507					
	Stem diameter	0.6212	0.5342					
	Tiller weight	0.5428	0.8668					
	Fresh weight	0.0648	3.3111					
	Head number	0.0613	1.8173					

APPENDIX 3. SELECTION INDICES FOR THE SIMULTANEOUS SELECTION ON HERBAGE AND SEED YIELD THE UNDERLINED VARIATE IS THE LEAST INFLUENTIAL OF EACH EQUATION AND WILL BE ELIMINATED IN THE NEXT STEP - CONTINUED

Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$5Y_{DM} + Y_{CL}$	Tiller number	0.2051	1.4231	27.7870	35.4156	0.7846	20.8k	30.5k
	Time of head emergence	0.8623	0.3424					
	Tiller angle	0.6086	0.6050					
	Tiller length	0.2455	0.9577					
	Leaf number	-0.1982	1.3459					
	Stem diameter	0.7273	0.7856					
	Tiller weight	0.6330	1.3127					
	Fresh weight	0.0666	3.5566					
	Head number	0.0609	1.8048					
$5Y_{DM} + Y_{CL}$	Tiller number	0.2152	1.5965	27.6918	35.4156	0.7819	20.7k	30.5k
	Tiller angle	0.6901	0.8097					
	Tiller length	0.2289	0.8490					
	Leaf number	-0.1953	1.3164					
	Stem diameter	0.5778	0.5521					
	Tiller weight	0.7703	2.3984					
	Fresh weight	0.0607	3.2293					
	Head number	0.0529	1.5059					
$5Y_{DM} + Y_{CL}$	Tiller number	0.2047	1.4697	27.5389	35.4156	0.7776	20.6k	30.3k
	Tiller angle	0.6930	0.8257					
	Tiller length	0.2216	0.8056					
	Leaf number	-0.2025	1.4373					
	Tiller weight	0.8926	3.6756					
	Fresh weight	0.0634	3.6125					
	Head number	0.0482	1.2878					
$5Y_{DM} + Y_{CL}$	Tiller number	0.1954	1.3651	27.3171	35.4156	0.7713	20.5k	30.1k
	Tiller angle	0.5589	0.5670					
	Leaf number	-0.1879	1.2680					
	Tiller weight	1.1331	9.2004					
	Fresh weight	0.0639	3.7232					
	Head number	0.0589	2.1330					
$5Y_{DM} + Y_{CL}$	Tiller number	0.1907	1.3165	27.1622	35.4156	0.7670	20.3k	30.1k
	Leaf number	-0.1904	1.3173					
	Tiller weight	1.1360	9.3610					
	Fresh weight	0.0626	3.6235					
	Head number	0.0565	1.9942					
$5Y_{DM} + Y_{CL}$	Leaf number	-0.1448	0.8283	26.8046	35.4156	0.7569	20.0k	29.9k
	Tiller weight	1.0522	8.5276					
	Fresh weight	0.0776	6.8876					
	Head number	0.0742	4.2088					
$5Y_{DM} + Y_{CL}$	Tiller weight	0.9262	7.7998	26.5826	35.4156	0.7506	19.9k	29.2k
	Fresh weight	0.0759	6.7297					
	Head number	0.0749	4.3574					
$5Y_{DM} + Y_{CL}$	Tiller weight	0.6895	5.2688	25.4243	35.4156	0.7179	19.3k	26.7k
	Fresh weight	0.1151	32.7956					
$5Y_{DM} + Y_{CL}$	Fresh weight	0.1349	100.0000	24.0847	35.4156	0.6801	18.1k	26.1k

APPENDIX 3. SELECTION INDICES FOR THE SIMULTANEOUS SELECTION ON HERBAGE AND SEED YIELD THE UNDERLINED VARIATE IS THE LEAST INFLUENTIAL OF EACH EQUATION AND WILL BE ELIMINATED IN THE NEXT STEP - CONTINUED

Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$Y_{DOM} + 5Y_{GS}$	Tiller number	0.8643	5.9902	61.5284	96.9824	0.6344	18.4k	36.7k
	Time of head emergence	6.9816	5.0809					
	Tiller angle	-0.2962	0.0286					
	Tiller length	1.0101	3.4061					
	Leaf number	-0.6846	3.0978					
	Leaf width	0.3138	0.6858					
	Leaf length	-1.5032	1.1649					
	Stem diameter	1.2335	0.4447					
	Tiller weight	1.0517	0.6225					
	Fresh weight	0.1441	3.5322					
$Y_{DOM} + 5Y_{GS}$	Tiller number	0.8689	6.0960	61.5108	96.9824	0.6342	18.4k	36.7k
	Time of head emergence	6.8980	5.0892					
	Tiller length	1.0240	3.5847					
	Leaf number	-0.6864	3.1184					
	Leaf width	0.3123	0.6800					
	Leaf length	-1.5348	1.2377					
	Stem diameter	1.2254	0.4393					
	Tiller weight	1.0574	0.6299					
	Fresh weight	0.1442	3.5390					
$Y_{DOM} + 5Y_{GS}$	Tiller number	0.8312	5.7647	61.2406	96.9824	0.6315	18.4k	36.6k
	Time of head emergence	6.3607	4.6775					
	Tiller length	0.9974	3.4470					
	Leaf number	-0.6731	3.0319					
	Leaf width	0.3760	1.0648					
	Leaf length	-1.4084	1.0710					
	Tiller weight	1.3052	1.0533					
	Fresh weight	0.1395	3.3674					
$Y_{DOM} + 5Y_{GS}$	Tiller number	0.7421	4.9806	60.5955	96.9824	0.6248	18.2k	36.2k
	Time of head emergence	7.4432	7.6016					
	Tiller length	1.3141	9.3512					
	Leaf number	-0.5305	2.1966					
	Leaf width	0.5223	2.4956					
	Leaf length	-0.9590	0.5643					
	Fresh weight	0.1611	4.9997					
$Y_{DOM} + 5Y_{GS}$	Tiller number	0.7270	4.8476	60.2536	96.9824	0.6213	18.8k	35.9k
	Time of head emergence	6.9254	7.0832					
	Tiller length	1.2822	9.0757					
	Leaf number	-0.4932	1.9553					
	Leaf width	0.4669	2.1173					
	Fresh weight	0.1481	4.5184					
$Y_{DOM} + 5Y_{GS}$	Tiller number	0.6612	4.2439	59.0755	96.9824	0.6091	18.8k	35.1k
	Time of head emergence	6.1049	5.9905					
	Tiller length	1.1116	7.6497					
	Leaf width	0.4691	2.2249					
	Fresh weight	0.1422	4.3444					
$Y_{DOM} + 5Y_{GS}$	Tiller number	0.5773	3.4766	57.7611	96.9824	0.5956	18.5k	34.3k
	Time of head emergence	6.6277	7.5941					
	Tiller length	1.1472	8.5937					
	Fresh weight	0.1701	7.1293					

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Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$Y_{DOM} + 5Y_{GS}$	Time of head emergence	6.2426	7.2717	55.7529	96.9824	0.5749	18.1k	33.1k
	Tiller length	1.1033	8.5594					
	Fresh weight	0.2358	22.9079					
$Y_{DOM} + 5Y_{GS}$	Tiller length	1.2232	12.6809	51.6987	96.9824	0.5331	18.5k	30.5k
	Fresh weight	0.1861	18.5852					
$Y_{DOM} + 5Y_{GS}$	Fresh weight	0.2529	100.0000	45.1428	96.9824	0.4655	17.7k	26.4k
$Y_{DOM} + Y_{GS}$	Tiller number	0.4925	4.3473	38.3110	56.3777	0.6795	19.2k	36.4k
	Time of head emergence	3.7808	3.5434					
	Tiller length	0.5810	2.8151					
	Leaf number	-0.3739	2.3518					
	Leaf width	0.1703	0.5205					
	Leaf length	-0.6088	0.4964					
	Stem diameter	0.8265	0.4893					
	Tiller weight	0.6566	0.6199					
	Fresh weight	0.0902	3.3542					
	Head number	0.0166	0.0696					
$Y_{DOM} + Y_{GS}$	Tiller number	0.5154	5.5198	38.2844	56.3777	0.6791	19.1k	36.5k
	Time of head emergence	3.6170	3.5846					
	Tiller length	0.6016	3.1871					
	Leaf number	-0.3805	2.4656					
	Leaf width	0.1692	0.5145					
	Leaf length	-0.5889	0.4686					
	Stem diameter	0.7563	0.4320					
	Tiller weight	0.6346	0.5856					
	Fresh weight	0.0934	3.8396					
$Y_{DOM} + Y_{GS}$	Tiller number	0.4921	5.2002	38.1190	56.3777	0.6761	19.0k	36.3k
	Time of head emergence	3.2854	3.1967					
	Tiller length	0.5851	3.0560					
	Leaf number	-0.3723	2.3863					
	Leaf width	0.2085	0.8439					
	Leaf length	-0.5109	0.3625					
	Tiller weight	0.7876	0.9896					
	Fresh weight	0.0905	3.6644					
$Y_{DOM} + Y_{GS}$	Tiller number	0.4744	4.9512	37.9808	56.3777	0.6737	19.4k	35.9k
	Time of head emergence	3.1655	3.0216					
	Tiller length	0.6072	3.3593					
	Leaf number	-0.3377	2.0926					
	Leaf width	0.1992	0.7795					
	Tiller weight	0.6340	0.7195					
	Fresh weight	0.0869	3.4513					
$Y_{DOM} + Y_{GS}$	Tiller number	0.4346	4.4133	37.7075	56.3777	0.6688	19.1k	35.8k
	Time of head emergence	3.8092	5.4250					
	Tiller length	0.7683	8.2856					
	Leaf number	-0.2769	1.5709					
	Leaf width	0.2829	1.9836					
	Fresh weight	0.1003	5.3113					

APPENDIX 3. SELECTION INDICES FOR THE SIMULTANEOUS SELECTION ON HERBAGE AND SEED YIELD THE UNDERLINED VARIATE IS THE LEAST INFLUENTIAL OF EACH EQUATION AND WILL BE ELIMINATED IN THE NEXT STEP - CONTINUED

Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$Y_{DOM} + Y_{GS}$	Tiller number	0.3977	3.8815	37.1151	56.3777	0.6583	19.1k	35.0k
	Time of head emergence	3.3485	4.5317					
	Tiller length	0.6725	7.0717					
	Leaf width	0.2842	2.0665					
	Fresh weight	0.0970	5.1393					
$Y_{DOM} + Y_{GS}$	Tiller number	0.3468	3.1637	36.3481	56.3777	0.6447	18.8k	34.2k
	Time of head emergence	3.6652	5.8108					
	Tiller length	0.6941	7.9150					
	Fresh weight	0.1139	8.1091					
$Y_{DOM} + Y_{GS}$	Time of head emergence	3.4338	5.4691	35.1982	56.3777	0.6243	18.4k	33.0k
	Tiller length	0.6677	7.8350					
	Fresh weight	0.1534	24.5296					
$Y_{DOM} + Y_{GS}$	Tiller length	0.7336	10.9091	33.2732	56.3777	0.5902	18.6k	30.4k
	Fresh weight	0.1260	20.8274					
$Y_{DOM} + Y_{GS}$	Fresh weight	0.1661	100.0000	29.6434	56.3777	0.5258	17.7k	26.4k
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3261	2.8584	31.2902	41.4266	0.7553	20.3k	34.9k
	Time of head emergence	2.0461	1.5296					
	Tiller angle	0.3590	0.1655					
	Tiller length	0.3908	1.8734					
	Leaf number	-0.2176	1.2539					
	Leaf width	0.0946	0.2405					
	Stem diameter	0.7382	0.5980					
	Tiller weight	0.5303	0.6550					
	Fresh weight	0.0735	3.3837					
	Head number	0.0357	0.4865					
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3210	2.7894	31.2384	41.4266	0.7541	20.2k	35.1k
	Time of head emergence	2.1664	1.7791					
	Tiller length	0.3716	1.7457					
	Leaf number	-0.2177	1.2593					
	Leaf width	0.0968	0.2527					
	Stem diameter	0.7581	0.6346					
	Tiller weight	0.5341	0.6669					
	Fresh weight	0.0736	3.3983					
	Head number	0.0365	0.5093					
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3200	2.7875	31.1595	41.4266	0.7522	20.2k	34.9k
	Time of head emergence	2.1625	1.7817					
	Tiller length	0.3478	1.5799					
	Leaf number	-0.2313	1.4579					
	Stem diameter	0.8783	0.9149					
	Tiller weight	0.6358	1.0525					
	Fresh weight	0.0756	3.6490					
	Head number	0.0361	0.5011					
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3713	4.4528	31.0034	41.4266	0.7484	19.9k	35.1k
	Time of head emergence	1.8205	1.3964					
	Tiller length	0.3913	2.1304					
	Leaf number	-0.2482	1.7257					
	Stem diameter	0.7314	0.6744					
	Tiller weight	0.5970	0.9941					
	Fresh weight	0.0828	4.7646					

APPENDIX 3. SELECTION INDICES FOR THE SIMULTANEOUS SELECTION ON HERBAGE AND SEED YIELD THE UNDERLINED VARIATE IS THE LEAST INFLUENTIAL OF EACH EQUATION AND WILL BE ELIMINATED IN THE NEXT STEP - CONTINUED

Aggregate breeding value	X-variates	Index weight	Value (%)	σ_I	σ_H	r_{IH}	$G_{Y_{DM}}$	$G_{Y_{CL}}$
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3494	4.0804	30.7943	41.4266	0.7433	19.8k	34.9k
	Time of head emergence	1.4954	1.0204					
	Tiller length	0.3601	1.8637					
	Leaf number	-0.2510	1.7903					
	Tiller weight	0.8246	2.3075					
	Fresh weight	0.0813	4.6578					
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3522	4.2366	30.4800	41.4266	0.7358	19.9k	33.7k
	Tiller length	0.3063	1.4311					
	Leaf number	-0.2365	1.6300					
	Tiller weight	1.0601	4.8276					
	Fresh weight	0.0663	3.7124					
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3659	4.7404	30.0439	41.4266	0.7252	19.7k	32.9k
	Leaf number	-0.2225	1.4905					
	Tiller weight	1.3616	11.6028					
	Fresh weight	0.0722	4.6631					
$5Y_{DOM} + Y_{GS}$	Tiller number	0.3215	3.9363	29.5961	41.4266	0.7144	19.5k	32.1k
	Tiller weight	1.1417	10.3439					
	Fresh weight	0.0760	5.3826					
$5Y_{DOM} + Y_{GS}$	Tiller weight	0.9737	8.5461	28.4311	41.4266	0.6863	18.9k	30.3k
	Fresh weight	0.1176	26.3868					
$5Y_{DOM} + Y_{GS}$	Fresh weight	0.1457	100.0000	26.0013	41.4266	0.6276	17.7k	26.4k

APPENDIX 4. SUBSETS OF X-VARIATES WITHIN DIFFERENT AGGREGATE BREEDING VALUES

Aggregate breeding value	X-variates	Partial regression coefficient	t-value	Relative influence	F-value	R^2	RMS	G
Y_{DM}	Tiller angle	0.888	1.6	0.12				
	Tiller weight	0.350	1.4	0.13				
	Fresh weight	0.058	3.0	0.30				
	Constant	91.363			$F_{117}^{3} = 8.3^{**}$	0.175	72.860	4.5k
Y_{DM}	Time of head emergence	1.144	1.4	0.12				
	Tiller angle	0.802	1.4	0.11				
	Fresh weight	0.080	4.9	0.41				
	Constant	92.399			$F_{117}^{3} = 8.3^{**}$	0.175	72.864	4.5k
Y_{DM}	Time of head emergence	0.763	0.8	0.08				
	Tiller angle	0.804	1.4	0.11				
	Tiller weight	0.234	0.8	0.09				
	Fresh weight	0.067	3.1	0.35				
	Constant	91.039			$F_{116}^{4} = 6.4^{**}$	0.180	73.049	4.6k
Y_{DM}	Tiller angle	0.957	1.7	0.13				
	Tiller weight	0.390	1.6	0.14				
	Fresh weight	0.082	2.8	0.42				
	Y_{DM}	-0.028	1.1	0.16				
	Constant	90.445			$F_{116}^{4} = 6.5^{**}$	0.183	72.777	4.6k
Y_{DM}	Time of head emergence	1.220	1.5	0.13				
	Tiller angle	0.862	1.5	0.12				
	Fresh weight	0.103	3.6	0.53				
	Y_{DM}	-0.026	1.0	0.15				
	Constant	91.746			$F_{116}^{4} = 6.4^{**}$	0.182	72.895	4.6k
Y_{DM}	Tiller angle	0.936	1.6	0.13				
	Leaf number	-0.002	0.0	0.00				
	Stem diameter	-5.825	1.3	0.14				
	Tiller weight	0.581	1.8	0.22				
	Fresh weight	0.054	2.8	0.28				
	Constant	106.170			$F_{115}^{5} = 5.3^{**}$	0.188	72.969	4.7k
Y_{DOM}	Tiller number	0.004	0.1	0.01				
	Tiller length	3.339	3.1	0.48				
	Leaf width	2.221	0.2	0.04				
	Stem diameter	-2.010	0.1	0.01				
	Constant	55.166			$F_{45}^{4} = 3.3^{*}$	0.224	25.767	6.9k
Y_{DOM}	Tiller number	0.022	0.3	0.06				
	Tiller length	3.655	3.2	0.53				
	Leaf number	-0.908	0.9	0.15				
	Leaf width	2.737	0.3	0.05				
	Stem diameter	2.352	0.1	0.01				
	Constant	58.188			$F_{44}^{5} = 2.7^{*}$	0.237	25.922	7.1k
Y_{DOM}	Tiller number	0.002	0.0	0.00				
	Tiller length	3.467	3.0	0.50				
	Leaf number	-0.676	0.6	0.11				
	Leaf width	0.441	0.0	0.01				
	Leaf length	3.486	0.9	0.14				
	Stem diameter	-1.553	0.0	0.01				
	Constant	53.740			$F_{43}^{6} = 2.4^{*}$	0.252	26.007	7.3k
Y_{CL}	Y_{CL}	0.047	4.3	0.28				
	Constant	16.066			$F_{119}^{1} = 18.1^{**}$	0.132	8.553	5.3k
Y_{CL}	Tiller number	0.001	0.5	0.05				
	Head number	-0.012	1.3	0.16				
	Y_{CL}	0.054	4.0	0.33				
	Constant	16.797			$F_{117}^{3} = 6.6^{**}$	0.145	8.575	5.6k
Y_{CL}	Tiller angle	0.057	0.3	0.03				
	Head number	-0.010	1.1	0.12				
	Y_{CL}	0.055	4.2	0.34				
	Constant	15.949			$F_{117}^{3} = 6.5^{**}$	0.144	8.584	5.5k

APPENDIX 5. HERITABILITIES IN THE NARROW SENSE OF SELECTION INDICES (h^2_n) Timehe = time of head emergence; Fwplan = fresh weight of the plant; Headnb = head number; Yiedma = Yield of dry matter; Yiedom = Yield of digestible organic matter; Yiecle = Yield of clean seed; Yieger = Yield of germinating seeds.

Aggregate breeding value	Index variates	h^2_n
Y_{DM}	Timehe + Fwplan	0.250
	Timehe + Yiedma	0.191
	Fwplan + Yiedma	0.161
	Timehe + Fwplan + Yiedma	0.238
Y_{DOM}	Timehe + Fwplan	0.361
	Timehe + Yiedom	0.290
	Fwplan + Yiedom	0.236
	Timehe + Fwplan + Yiedom	0.372
Y_{CL}	Timehe + Fwplan	0.288
	Timehe + Headnb	0.243
	Timehe + Yiecle	0.091
	Fwplan + Headnb	0.086
	Fwplan + Yiecle	0.066
	Headnb + Yiecle	0.098
	Timehe + Fwplan + Headnb	0.212
	Timehe + Fwplan + Yiecle	0.056
	Timehe + Headnb + Yiecle	0.103
	Fwplan + Headnb + Yiecle	0.093
	Timehe + Fwplan + Headnb + Yiecle	0.049
Y_{GS}	Timehe + Fwplan	0.323
	Timehe + Headnb	0.208
	Timehe + Yieger	0.209
	Fwplan + Headnb	0.199
	Fwplan + Yieger	0.195
	Headnb + Yieger	0.154
	Timehe + Fwplan + Headnb	0.301
	Timehe + Fwplan + Yieger	0.292
	Timehe + Headnb + Yieger	0.202
	Fwplan + Headnb + Yieger	0.226
	Timehe + Fwplan + Headnb + Yieger	0.283

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