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Evaluation of Three Cycles of Recurrent Phenotypic Selection for Forage Yield in Orchardgrass and Timothy

By

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A thesis submitted to the Faculty of Graduate
Studies and Research in Partial fulfilment
of the requirements for the degree of
Master of Science

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Short title

Recurrent Phenotypic Selection
in Orchardgrass and Timothy

Djavad Shateryan

FOREWORD

The recurrent selection program evaluated in this thesis was carried out from 1983-1988 by my supervisor, Dr. B.E. Coulman. He established the first evaluation trials in 1989 and collected data in 1990 and 1991. I commenced my M.Sc. program in spring of 1992. I collected data on the 1989-seeded sward trials in 1992. I also established new evaluation trials in 1992 and collected data from these in 1993. To permit a more complete anaylsis of the selection program, Dr. Coulman provided me the data he had collected in 1990 and 1991. Thus all data collected from 1990-1993 are included in this thesis.

Abstract

Three cycles of recurrent restricted phenotypic selection (RRPS) were carried out on two cultivars each of timothy (*Phleum pratense* L.) and orchardgrass (*Dactylis glomerata L.*). The selections were conducted at the E.A. Lods Agronomy Research Center of Macdonald Campus of McGill University from 1984 to 1988. Individual plant selections were based on dry matter yields of 25 plants. Within each of 16 grids, the five highest yielding genotypes were selected (i.e. 80 genotypes overall) and allowed to interpollinate. Equal weights of seeds from each of the 80 selected plants were mixed in each cycle. Evaluation trials were carried out in both sward and spaced stand from 1989 to 1993 to assess the effectiveness of selection in improving dry matter yield. Several other morphological and physiological characteristics of cycles were recorded to find possible associated changes.

Three cycles of RRPS were not effective in increasing forage dry matter yields. The lack of response may be due to a narrow genetic base in the source populations and/or the population size under selection may have been too small, resulting in inbreeding depression. Another explanation for the ineffective selection may be non-random pollination among selected plants. The selection for forage yield produced some minor changes in other characteristics. There was a tendency towards increased plant height and circumference in orchardgrass; however, for timothy, height and circumference were reduced by selection. Cycle 3 of Avon orchardgrass was one day later in maturity and there was also a tendency for later maturity for timothy.

Résumé

Trois cycles de "recurrent restricted phenotypic selection (RRPS)" ont été effectués sur deux cultivars de mil (*Phleum pratense* L.) et de dactyle (*Dactylis glomerata* L.) , en utilisant un système de grille. La sélection a été conduite au Centre de Recherche Agronomique E.A. Lods du Campus Macdonald, université McGill, de 1984 à 1988. La sélection des plants individuels dans chaque parcelle a été basée sur leurs poids secs à la récolte (25 génotypes ayant chacun deux répétitions). Dans chaque parcelle, les 5 génotypes ayant les mesures de poids les plus élevées ont été sélectionnées (80 plants au total), et une pollinisation croisée a été permises entre ces plants. Un nombre égal de graines provenant de chaque plant sélectionné a été recolté à chaque cycle. Les essais d'évaluation ont eu lieu dans "sward and spaced stand" de 1989 à 1993 utilisant une technique de sous échantillonnage. Plusieurs autre caractéristiques morphologiques et physiologiques de chaque cycle ont été notées pour pouvoir détecter les "associated changes" possible. Trois cycles de "RRPS" ne sont pas parvenu à augmenter le rendement en fourrage. Ces résultats peuvent être expliqués par une diversité génétique trop faible dans nos populations initiales. La grandeur de la population sur laquelle la sélection a été effectuée était possiblement trop petite, donnant lieu à une "inbreeding depression". Une autre explication pour le manque d'efficacité de notre sélection peut être une déficience dans la distribution aléatoir du pollen entre les plants sélectionnés. La sélection a amené des changements mineurs à d'autres caractères. On a observé une tendance à l'augmentation de la

hauteur et de la circonférence des plants de mil. Le cycle trois de Avon (dactyle) a atteint sa maturité un jour plus tard. On a également observé une maturité plus tardive

chez le mil.

DEDICATION

To the farmers

To the patience of my wife

Acknowledgements

The author wishes to extend his sincere gratitude to Dr. B.E. Coulman and Dr. Diane E. Mather for their valuable guidance and advice during this investigation and also for their help in the preparation of the thesis.

Sincere gratitude is extended to the staff and students of the Department of Plant Science for their assistance in many ways, especially to Wendy Asbil, and Dr. P. Dutilleul, for their kind assistance and encouragement throughout the duration of this study.

Special acknowledgement is due to the Sugar Beet Seed Institute for the award of the Scholarship and for granting me leave for the tenure of this study.

Finally I thank God, who has helped and led me in my life-time.

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Chapter I

INTRODUCTION

The genetic improvement of forage crops has made a major contribution to the development of ruminant animal production. The grass family (Gramineae) includes approximately 75% of the species cultivated as forage crops (Metcalfe and Nelson,1985). The family is distributed throughout the world ranging from subpoiar regions to the tropics. Therefore breeders have access to wide ranges of adaptation, both within and between species. Forage grasses are categorized into two large groups: warm and cool-season grasses. Warm-season grasses produce most of their growth during the warmer periods of the growing season, while cool-season species are productive in spring and fall.

Forage breeding, especially grass breeding, is new in comparison to cereal improvement programs. Applying a more effecient breeding program and developing cultivars with high herbage yield of superior quality are the goals of most forage grass breeders. Herbage yield is under the control of many genes, and the heritability for the trait is low; thus in numerous reports, the improvement in forage yield under selection has been slow.

Among different methods used in crop breeding, phenotypic mass selection has been considered to be one of the procedures which is suitable for new breeding programs, or for variety maintenance, where it used to rogue poor or off-types. Gardner (1969) applied a modified form of phenotypic selection, recurrent restricted phenotypic selection (RRPS), to increase the grain yield of maize (*Zea mays* L.) by 38%. This achievement encouraged other breeders to reconsider recurrent phenotypic selection. Burton (1974) and Werner and Burton (1991) imposed several restrictions to selection in Pensacola bahiagrass (*Paspalum notatum* L.) (a warm-season grass) to reduce the adverse effect of soil heterogeneity on the selection of plants and provide effective intercrossing. By doing this, they had unexpected success in increasing forage yield. Thus, according to the recent literature (Burton, 1992), RRPS is an effective breeding method for increasing the frequencies of desirable genes and gene complexes for desirable crop characteristics.

In the present study, the main objective was to evaluate the effect of three cycles of recurrent phenotypic selection for forage dry matter yield of two cultivars of timothy (*Phleum pratense* L.) and orchardgrass (*Dactylis glomerata L.*). The evaluation was carried out under spaced-plant and sward conditions. Forage dry matter yield was measured to assess the direct effect of selection while several other characters were measured to assess indirect effects. These included seed yield, maturity, winter hardiness, plant morphology, plant height and plant circumference.

Chapter II

LITERATURE REVIEW

2.1 History of Grass Breeding

There are more species in the grass family than any other plant family and most are polyploid. Many of the world's most important forages are cool-season grasses which grow rapidly and start flowering when temperatures are moderate. Two conditions are required (Barker and Kalton, 1989) to use grassland more efficiently: (i) proper field management, and (ii) use of species and cultivars adapted to the specific climate and uses.

Selection and improvement of grasses go back to prehistoric times before the appearance of humans. Since the time of the appearance of grazing animals, grass species were exposed to animal and natural selection. According to biblical records, grasses and grasslands were mainstays for human survival (Heath et al., 1985). However, grass breeding as an applied biological science is relatively young compared to cereal breeding (Van Bogaert, 1977). There were reports of "strain building" in the 1920s, but before that time germplasm work involved only collection, introduction, and evaluation of species.

At the starting point of forage improvement, there was little genetic information about important grasses which are currently in use in the animal industry. Many species were evaluated for adaptation and usage as forage crops and the data recorded in annual reports (Dillman, 1946). Collections of exotic species were carried out and then introduced into the USA for further evaluation in specific environments. In the late 1800s and early 1900s, N.E. Hansen, a famous plant explorer, made collection trips into Siberia. Many of his original introductions of grasses served as the genetic base for cultivars still in use in grass breeding programs (Barker and Kalton, 1989).

Major progress in grass breeding work was not reported until the middle of the 1930s. At that time, a number of forage researchers were making selections among strains and land races (Breese and Davies 1969). Early forage grass breeders were concerned about the same constraints in breeding grasses that are experienced today. To achieve the objectives of a specific program, breeders have to find sources of heritable variation, and develop techniques for rapid screening of important plant traits. The majority of forage grasses are perennial plants which complicates the measurement and evaluation of forage yields. Moreover, high ploidy levels cause the genetics and breeding of many grasses to be more difficult than for diploid species. The major roadblocks of grass breeding are clearly documented today, and by the utilization of advanced genetic knowledge, progress is being made in forage improvement. Some breeding programs are using some form of recurrent restricted phenotypic selection (Burton, 1982) to increase frequencies of favourable genes for specific traits within grass populations. Others are conducting top-cross progeny programs to evaluate combining ability for desired traits to select superior clonal material for synthetic varieties. However, progress from selection for increased forage yield has been difficult in many species (Van Bogaert, 1977) and progress has been especially slow in cool-season grasses. Only when selection has been made for survival or adaptation to particular environmental conditions (for example, crested wheatgrass, *Agropyron caninum*, L. and Russian wildrye, *Elymus sp.* L., have major break throughs been achieved in forage yield (Barker and Kalton, 1989).

Part of the reason for the slow improvement of forage yield is the dynamic nature of forage dry matter accumulation. There is no specific time, as in the case of cereals, at which maximum yield is reached and can be fully evaluated. Moreover, there is a lack of coordinated work among researchers for cultivar evaluation. This kind of work has been difficult because of large environmental differences among test sites and the expense of conducting multiple location evaluations of forages. Thus, few regional testing programs exist (Barker and Kalton, 1989). While many forage grass breeding programs have higher forage yield as the goal, dry matter yield is not as important as is yield of digestible dry matter or yield of digestible energy. Each grass species has a different pattern and rate of digestible dry matter accumulation and it has been reported that genetic differences exist within species. There is a major problem in selecting both for high forage yield and high forage quality (Newell and Moline, 1978). It has been documented that forage yield increases while forage quality components decrease through the growing season. Measurement of forage yield and quality is more complicated when a genotype X time interaction occurs. Selection for higher forage yield usually is correlated with lower quality; however, selection for higher quality without significant changes in forage yield has been reported (Casler and Ehlke, 1986; Casler, 1986; Barker and Kalton, 1989).

2.2 Selection Procedures

Mass selection is based on the phenotype of the maternal parent. Generally, characters of high heritability can be effectively improved through mass selection. However, characteristics with low heritability, such as yield, have been difficult to improve under mass selection (Allard 1960; Gardner 1969). Under mass selection, selected plants are pollinated by both selected and unselected plants and there usually is no specific environmental restriction.

Several methods of recurrent selection have been suggested. Some involve progeny testing; others rely only on the performance of the parents. Briggs and Knowles (1967) recognized and described four types of recurrent selection: (1) recurrent selection for phenotype; (2) recurrent selection for general combining ability; (3) recurrent selection for specific combining ability; and (4) reciprocal recurrent selection. Recurrent phenotypic selection for forage yield provides the opportunity to make a stepwise improvement in populations of cross pollinating crops. With each cycle of selection, the frequency of desirable genes increases in the population (Allard 1960). Recurrent restricted phenotypic selection (RRPS) is mass selection modified by restrictions which make it more efficient and more promising (Burton 1974). RRPS restricts the pollen source to the selected phenotypes and provides a more even and effective pollination than generally occurs in recurrent selection.

RRPS imposes some restrictions to the environment of the plant, under which the phenotypes are selected, to make it more uniform (Barker and Kalton, 1989). Depending on the nature of the species, some of the following restrictions to recurrent phenotypic selection are recommended (Burton, 1992):

1) Dividing a space-planted nursery into sub-areas and selecting visually a fixed number of the best plants (for example 20 percent) in each area. This plant grid reduces soil heterogeneity effects on selection and facilitates visual selection,

2) Saving at least 20% of the plant population for the next cycle retains genetic variability, delays loss of vigour due to inbreeding depression and reduces the possibilities of overlooking high-yielding plants.

3) Intermating selected phenotypes only with each other in isolation. The progress realized from mass selection should be doubled if only selected plants are intermated.

4) Collecting equal numbers of seeds from each selected plant to ensure equal representation of each entry.

Among breeding methods other than RRPS, synthetic variety development has been the method generally used to improve the yield and performance of forages. However, this method lacks the potential cumulative changes that can be brought about by recurrent selection. Since there are usually no significant disease or insect problems in cool-season grasses, forage yield is usually the focus of selection. Another alternative to RRPS would be development of two-clone hybrids; however this method involves considerable labour to produce propagules and plant them in a seed production field. The lack of a mechanical method for doing this restricts the use of these hybrids to experimental fields. Scheller (1976) evaluated the effect of different numbers of timothy clones in producing synthetic varieties. Four kinds of synthetic varieties generated from 2, 3, 5 and 24 clones were examined for yield and growth form. In the first (syn-1) generation, the yield of the 2- and 3-clone synthetics were higher than the 5-and 24 clone synthetics. However, in the second and third generations, syn2 and syn3, there was little difference in yield among four synthetics. The total forage yield of orchardgrass was evaluated comparing several kinds of variety synthesis: conventional synthetic (CS), restricted polycross (RP), single-cross synthetic from selfed progeny of each parental clone (S1 X S1), single-cross S1 progeny intercrossed in isolations (S1F1 X S1F1) and double-cross synthetics from Syn1, S1 X S1 and S1F1 X S1F1 single crosses. Yields and protein percentage decreased as inbreeding level increased from RP to S1 X S1 and S1F1 X S1F1. Inbreeding did not affect the expression of general combining ability among clones.

2.3 Response to recurrent phenotypic selection

There are a number of studies that successfully applied RRPS in warm-season grasses. Forage yield of Pensacola bahiagrass was improved using a selection intensity of 20% in three cycles of RRPS (Burton, 1974). In a narrow gene pool (NGP), the gain was 2% per cycle and in a wide gene pool (WGP), 6% per cycle. Both populations, after three cycles of improvement, yielded 16 to 19% more forage than the commercial check variety. The coefficients of variation for dry-matter yields of spaced plants of the original and fourth-cycle populations evaluated in the same test showed that three cycles of selection reduced the variability of the WGP to the level of the NGP population. However the variability of the NGP population, after four cycle of breeding, was as high as in the beginning. This suggests that applying RRPS to these populations would permit additive improvement in forage yield over several cycles. In conclusion, it was proven that an effective breeding program for yield increases both the yield of individual plants, and the frequency of such plants, as long as the breeder keeps the population size large enough to avoid inbreeding depression (Burton 1974).

Werner and Burton (1991) improved recurrent restricted phenotypic selection in bahiagrass with restrictions which permitted one cycle per year, and reduced the time required per cycle by half. The most important factor in this program was the use of cut stems of selected plants to produce seeds for the next cycle. This improved RRPS was four times more efficient than ordinary mass selection and cycle 6 gave 84% more yield than the control in a sward stand (Burton, 1982). Sixteen cycles of RRPS for yield significantly altered culm and leaf weight and length of Pensacola bahiagrass. It was suggested that selection in breeding nurseries be based on measurable morphological and physiological characters rather than visual selection (Werner and Burton, 1991).

Recurrent phenotypic selection (RPS) used to improve resistance to brown leaf spot in smooth bromegrass (*Pyrenophora bromi*) showed acceptable improvement in the fourth cycle (Berg et al., 1986). In red clover (*Trifolium pratense* L.) the effect of six cycles of phenotypic recurrent selection for stem length was studied (Bowley et al., 1984). The increase in stem length was associated with other changes in plant morphology and physiology such as plant persistence, stem number and yield per stem, which indicates that changes in root and crown development had occurred. The effectiveness of three cycles of selection in zigzag clover (*Trifolium intermedium* L.) was evaluated over a two-year period in an experiment using RPS (Taylor et al., 1984). Recurrent selection was effective in increasing vigour, seeds per head, heads per plant, and seeds per plant and a significant linear increase over cycles was found for each character.

2.4 Orchardgrass

2.4.1 Taxonomy

Dactylis is a small genus in Festuceae of the grass family. The name of the genus is derived from the greek word "dactylis", which means finger, and refers to the shape of the spikes. The best known species in the genus is *Dactylis glomerata* L., common orchardgrass (Heath et al., 1985). Orchardgrass is considered an autotetraploid species ($2n = 28$). Lentz et al., (1983) reported both tetrasomic and disomic segregation patterns for reaction to the stem rust fungus, *Puccinia graminis* Per f. sp.*dactylidis* Guyot et Massenot.

2.4.2 Plant description

Orchardgrass is a cool-season grass, which begins its growth at low temperature (minimum is 2°C) in spring. Flowering time occurs in late May or June, depending on the cultivar and temperature. Orchardgrass inflorescences range in length from 8 to 15 cm and consist of spikelets with two to five florets (Core et al., 1944). The lowest branches of the inflorescence are longer and more branched than those near the top. Leaf colour varies from light green to dark blue-green. As in the other grasses, orchardgrass has a fibrous root system. Orchardgrass can be propagated both sexually by seeds and asexually by tiller formation. At any stage of growth, tillers can be at various stages of development (Jung and Baker, 1968). This continuous tillering and the ability to accumulate carbohydrates in the crown near the soil surface allow it to survive as a perennial plant.

2.4.3 Origin, Distribution and Adaptation

Orchardgrass is known to be native to Europe, including Sweden, France, Switzerland, and Portugal (Creber, 1993). It has a fairly large range of adaptation, from the border of the Sahara desert to the subpolar zones (Stebbins and Zohary, 1959). However orchardgrass has sub-centers of development, for example in the former USSR for late maturing accessions (Casler, 1991), and in Australia for more tolerance to aluminium (Edmeades, 1991). European varieties are also tolerant to aluminium. Orchardgrass is grown to a limited extent in British Columbia and other agricultural regions of the western zones of Canada. It has been used over the large grassland area of the USA because of its importance to the animal industry. Orchardgrass is scattered to the northern part of Asia and at high latitudes of Africa (Piper 1942). Ancestors of *Dactylis* which may be of interest for breeding programs can be found in different habitats from the Atlantic coasts of Europe and north Africa, to Siberia and Tibet (Stebbins and Zohary 1959). Although orchardgrass is not native to North America, it has been found there for over

200 years, having been brought and scattered by Europeans.

2.4.4 Environmental Effects on Growth

Optimum temperature for orchardgrass growth is suggested to be 21°C. Because of its wide range of adaptation, orchardgrass has different optimum day-night temperature combinations. However, a 22/12°C (Baker et al., 1968) combination is usually accepted as being optimal. Temperatures above 28°C have drastic effects on plant development, tillering, growth and nucleic acid content of the leaves of orchardgrass; however it is more heat tolerant than timothy. Orchardgrass produces fairly good yield during spring and late fall, but it is usually outyielded by tall fescue. Because orchardgrass is susceptible to low temperature injury, especially when snow cover is lacking (Wilkinson and Gross, 1964; Sheaffer et al., 1981), it is usually replaced by timothy at higher elevations. Unlike other C_3 grasses, such as wheat and oats, the rate of photosynthesis of orchardgrass is fairly constant, and it yields as well in 30% of full sunlight as at higher light intensities. If moisture and nutrients are sufficient the canopy reaches an LAI of 5, two weeks after each cut, and can intercept 95% of sunlight (Pearce et al., 1965). Orchardgrass is known to be drought tolerant, but it does not tolerate flooding. It produces reasonable yields in poorly drained, or shallow, infertile soils but it is very responsive to fertilizer, especially nitrogen. Wherever nutrients , light and moisture are abundant, it becomes competitive, reducing legume content of swards and preventing weed establishment.

2.4.5 Harvest and Use

Orchardgrass is one of the most adapted grasses for use as pasture, hay, or green chop, and it can be utilized alone or in mixture with legumes. When high quality is the focus, orchardgrass should be harvested at head emergence. Because of the limited time of plant growth, the quality of the second cut, and subsequently the third cut, depends on the time of the first harvest. The choice of proper harvesting time for the first cut depends on the use of the forage (Heath et al., 1985).

2.5 Timothy

2.5.1 Taxonomy

Phylogenetic relationships of timothy are not well known. The number of species within *Phleum* has been suggested to be ten. Timothy is considered (Nath, 1967) a polyploid species, containing plants of varying degree of ploidy level from diploid to tetraploid. Available evidence has shown that common timothy should be considered as an autohexaploid ($2n=42$) of diploid *P. bertollonii* (previous name *P. nodosum*). Turf timothy, *P. bertolonii* DC. (*P. nodosum L.*), a diploid with 14 chromosomes, is morphologically very similar to *P. pratense*. Alpine timothy, *P. alpinum L.* (*P. commutatum Gaud.*), is a tetraploid with 28 chromosomes and can hybridize with cultivated timothy with some difficulty (Cai and Bullen, 1991; Heath et al., 1985).

2.5.2 Plant Description

Timothy is a cool-season perennial grass. It has a spikelike inflorescence with one flower in each spikelet. It grows in a bunch, and has long, flat leaves. Its culms are erect and cylindric and the height of cultivated timothy ranges from 80 to 110 cm. Unlike other grasses, timothy produces a haplocorm or corm from swollen internodes of the basal culm. New shoots grow from buds under the haplocorm. Although timothy shoots are biennial, the plant remains a perennial through the development of new shoots from culm bases (Langer 1956). Timothy produces a shallow fibrous root system (Heath et al., 1985).

2.5.3 Origin, Distribution and Adaptation

Timothy is thought to be a native of Europe and Asia, but different cultivars of timothy can be found in temperate and semi-arctic climates. It is present in all northern countries of Europe and is grown in South America and in Australia (Gregor and Sansone, 1930; Hanson, 1972). The historical migration of timothy goes back to the early settlement of Europeans in North America, when it was scattered and established by European pioneers in hay, and cargo residues cleaned off the ships (Edwards 1948).

The historical usage of timothy in North America goes back to the beginning of settlements in New England (Piper and Bort, 1915). The pioneers used timothy and called it herd grass after John Herd. Timothy Hanson had a major role in timothy's introduction as a forage crop in several states and the grass became known by his first name. Timothy is now found in coastal regions of North America and in Alaska. In Canada, it is grown in the eastern provinces and more humid areas of the west (Winter and Guta,1983; Darisse and Drapeau 1982; Veira et al., 1982; Lovering and McIsaac, 1981). Timothy is well suited to cool, humid conditions.

The optimum temperature for timothy growth, determined in growth chambers, is between 18.3 and 21.6°C with a night-day temperature range from 10-15°C to 15-21°C (Balasko and Smith, 1971). As with other cool-season grasses, day-length alters the time required for heading, anthesis and maturity (Heath et al., 1985).

2.5.4 Importance and Use

Timothy is grown primarily for hay or haylage and is suitable in Ontario and Quebec for mixtures with alfalfa for early cut haylage; it is generally included in mixtures for pasture. It is a noncompetitive grass; thus it adds to the yield and ground cover of a mixture without reducing the legume's yield or persistence. Timothy is one of the most widely grown forage crops in northern regions where it is well adapted. It has been shown that timothy silage is equal to corn silage for milk production. Timothy gives maximum dry matter yields when it is harvested at postbloom stage (Evans and Thatcher 1938; Brown et al., 1968). However quality is low at this advanced stage and a reasonable compromise between yield and quality is to cut at the heads emerged stage (Heath et al., 1985).

Chapter III

Materials and Methods

3.1 Selection Nurseries

Recurrent phenotypic selection was carried out on two cultivars each of timothy and orchardgrass. The timothy cultivars were Salvo, which is early maturing, and Drummond, which is late maturing. The orchardgrasses were the early maturing Avon and the later maturing Pennlate. All four cultivars are quite well adapted to the growing conditions of southern Quebec.

The selections were conducted at the E.A. Lods Agronomy Research Center of Macdonald Campus of McGill University, located at the west end of Montreal Island. The geographical location is 45°25'N and 73°56'W, at an altitude of approximately 330 meters above sea level. Nurseries were planted on two soil types: range 102, a Chicot fine sandy loam, and range 923, a Ste. Rosalie clay, both having pH of approximately 6.2. Nurseries were established on clean land, ploughed the previous autumn. Fertilizer (N-P_2O_5-K_2O) was applied at the rate of 20-100-100 kg ha^{-1} before transplanting, 0-35-70 kg ha^{-1} the 1st week in September and 60-30-30 kg ha^{-1} the year following establishment.

In the spring of 1983, seedlings of each population were established in the greenhouse in small plastic cells containing a mixture of sterile sand, loam and peat moss (1:1:1). Two weeks before transplanting, seedlings were moved to a cold frame outside the greenhouse for plant acclimation. Four hundred seedlings were transplanted to a breeding nursery with 2 m spacing between rows and 1 m between plants within rows.

In August of the establishment year (the various cycles of selection were established in 1983, 1985, 1987), when the plants had obtained a reasonable circumference (approximately 15 cm), each was split in half with a shovel. One half of the plant was uprooted and transplanted one meter away, beside the original plant. The nurseries then consisted of 800 plants all spaced one meter apart from each other. By the spring of the year after establishment, the duplicate plants were approximately equal in circumference.

3.2 Dry matter yield determination and selection

In the year after establishment (in years 1984, 1986 and 1988), when the plants had headed, but not flowered, one of the duplicates of each genotype was harvested with a sickle and weighed. Selection was carried out on a "grid" basis. The field was subdivided into 16 areas of 50 plants each (25 genotypes in duplicate) and within each area the five highest yielding genotypes were selected, a 20% selection intensity. This was done to minimize the effect of differential soil fertility within the experimental area. Over the entire nursery, twenty percent (80 plants) of the genotypes with the highest dry matter yield were selected and the uncut duplicate plants were allowed to flower and interpollinate. The duplicates of the eighty percent (320) unselected genotypes were cut back prior to flowering so that they would not interpollinate with the selected plants. Seed was harvested from each plant and equal quantities bulked to produce the selected seed from this cycle of selection. The flowering time of Pennlate was 7-10 days later than Avon, and Drummond was 10-14 days later than Salvo. Because of these differences, the nurseries of the two varieties were not always isolated as there was minimal risk of interpollination. The reason for duplicating the plants was to permit selection and production to take place in one year, the year after establishment. Timothy, and particularly orchardgrass, do not produce many inflorescences after being cut. Thus, if only single plants were established, they would not produce sufficient seed in the regrowth after being cut and seed would have to be harvested the following season. This would have increased the time required to complete one cycle of selection from two to the three years. Three cycles of the above mentioned selection, Recurrent Restricted Phenotypic Selection (RRPS), were carried out (cycle 1 - 1983,84; cycle 2 - 1985,86; cycle 3 - 1987,88). Seed from the previous cycle of selection was used to establish the nursery for the next cycle.

3.3 Evaluation Trials

The effectiveness of selection was evaluated in two types of trials, sward and spaced plants. Selection were made under spaced planted conditions; thus evaluation was done under similar conditions. On the other hand, these grasses will ultimately be grown in swards; thus evaluation must be carried out under these conditions as well.

3.3.1 Swards

The experimental fields received ($N-P_2O_5-K_2O$) fertilizer at the rate of 20-100-100 kg ha^{-1} before seeding, 0-35-70 kg ha^{-1} the 1st week in September and 60-30-30 kg ha^{-1} the following spring. The experiments were set up in a randomized complete block design (RCBD) with four replicates. Each replicate contained the original (cycle 0) cultivars and the three selected populations (cycle 1, 2, and 3). Each plot was 1.5 m in width and 5 m in length. The experiments were established in May of 1989 and 1992 (because of winter killing, the field trial was renewed in 1992). Two or three dry matter harvests per season were taken in 1990, 1991, 1992 and 1993. Each harvest was taken only from the middle of the plot, i.e. 60 or 100 cm width (depending on availability of harvesting equipment) and 4 m length. Semi-automatic or self-propelled harvesters (Buker, 1967) were employed. All plots were cut in the same day and were immediately weighed, using electronic scales. After having weighed the whole cut of each plot, a 500 g random sample was collected and dried at 60°C. Dry matter calculations were done on the basis of these samples. The height of the sward was also recorded using a meter stick placed at random at two or three places within each plot.

3.3.2 Spaced planted nurseries

Fertilizer application for the spaced planted nursaries were the same as those for the sward experiments. Greenhouse grown seedlings were established in a randomized complete block design with eight replicates. The same populations (cycles 0 to 3) were evaluated. Each plot consisted of a ten-meter row containing ten plants, one meter apart from each other and from plants of the adjacent plot. Data were collected on individual plants. The spaced plant nurseries were established in different years, 1989 and 1992,. The 1989 trial was evaluated in 1990, 1991 and the 1992 trial in 1993.

The following agronomic characters were measured on individual plants:

1) Forage Dry Matter Production

At approximately heading stage, five plants from each plot were cut by sickle and individually weighed. A 500 g sample was taken from each plot and dried in a forced air oven at 60°C, on the basis of these samples, dry matter yield ha^{-1} for each cultivar was computed. Three cuts of orchardgrass and two cuts of timothy were collected during each growing season.

2) Plant Height

The most predominant culm heights were measured at the heading stage with a meter stick.

3) Plant Circumference

This was measured at the heading stage 10 cm above the ground level.

4) Plant Maturity

On June 2, 1993 (for orchardgrass) and on June 8, 1993 (for timothy), the percentage heading was estimated for each plot. From this information, the dates on which 75% heading had occurred (or would occurr) were estimated. These heading dates were expressed in numbers of days from March 28, 1993 (the date on which the temperature first reached the minimum growth temperature of 2°C) (according to Simon and Park 1983).

5) Plant Persistence

The number of living plants per plot was recorded in May of each year.

6) Seed Yield

The five plants in each plot that were not harvested for forage dry matter yield were allowed to mature seed. Heads were harvested, dried, threshed, and the clean seed weighed.

3.4 Statistical Analysis

3.4.1 Analysis of Variance

The analysis of variance for the randomized complete block design was calculated according to the procedures outlined by Steel and Torrie (1980). The SAS (Statistical Analysis System) package was used to analyze data and the Duncan's Multiple Range Test was employed to compare the means of populations when F Values were significant ($P \leq 0.05$). Two types of analyses were performed:

(1) The plot mean for each character was used for the statistical analysis.

The form of the ANOVA and associated expected mean square for populations are presented in Table 3.1.

(2) In spaced plant trials, data from each individual plant were used in the analysis. This was in order to determine if the variation within populations was greater or smaller than that between populations. The form of the ANOVA for the second type of analysis is also presented in Table 3.1. The linear models assumed for each of the variables were as follows:

(a) for the plot mean data:

$Y_{ij} = \mu + R_i + G_j + E_{ij}$

(b) for data on individual plants

$Y_{IJK} = \mu + R_i + G_j + E_{ij} + S_{ijk}$

where

Y_{ij} = The effect due to jth cultivar in the ith replication;

Y_{ijk} = The effect due to the kth plant in the jth cultivar in the ith replication;

μ = The effect due to the overall mean;

R_i = The effect due to the ith replication, $i = 1,2,....,r$;

G_j = The effect due to the jth cultivar, $j = 1,2,....,g$;

E_{ij} = The effect due to error associated with the jth cultivar in the ith replication;

S_{ijk} = The effect due to error associated with the kth plant in the jth cultivar in the ith replication.

Replications (Blocks) were considered random and differences between blocks and cycles were tested using the block*cycle mean square (Table 3.1).

Table 3.1 Form of the analysis of variance and mean square expectation

Source of variation	Degrees of freedom	Mean square expectation	
		Plot Mean	Individual plant
		$Yij = \mu + Ri + Gj + Eij$	$Yijk = \mu + Ri + Gj + Eij + Sijk$
Block	r-1	$\sigma^2_e + g\sigma^2_r$	$\sigma^2_e + p\sigma^2_c + gp\sigma^2_r$
Cycle	g-1	$\sigma^2_e + r\sigma^2_k$	$\sigma^2_e + p\sigma^2_c + rp\sigma^2_g$
Block*Cycle	(r-1)(g-1)	σ^2_e	$\sigma^2_e + p\sigma^2_c$
Subsample	rg(k-1)		σ^2_e

3.4.2 Homogeneity of variance

The Bartlett test was used to compare variances of traits over several years (Steel and Torrie, 1980). If the computed Chi-Square for the variances of the trait is significant, data from each year have to be kept separate. When the Chi-Square is non-significant, cultivars can be compared across years. The suggested formula is as follows:

$X^2 = \{\Sigma(n_i-1)\ln S^2 - \Sigma(n_i-1)\ln S_i^2\}$; where

S^2 = Mean of pooled variances from several years;

$\ln S^2$ = Natural logarithm of variance;

S_i^2 = Variance from each year;

n_i = Number of observations.

3.4.3 Linear regression and correlation

Analysis of variance for linear regression was computed according to the guidelines for linear regression recommended by Steel and Torrie (1980). PROC REG from SAS program was applied to analyze coefficients of regression. The forms of the analysis of variance and associated mean square for traits are presented in Table 3.2.

Table 3.2. Analysis of covariance

Source of variation	Degree of freedom	Symbolic SS	Mean Square
X	1	$(\Sigma XY)^2/\Sigma X^2$	$(\Sigma XY)^2/\Sigma X^2$
Residual	N-2	$\Sigma Y^2-(\Sigma XY)^2/\Sigma X^2$	$[\Sigma Y^2-(\Sigma XY)^2/\Sigma X^2]/N-2$
Total	N-1	ΣY^2	$\Sigma Y^2/N-1$

X = Independent variable

N = Number of observations

Total = The sum of squares of dependent variable

Correlation coefficient estimates were computed by using PEARSON PROC CORRELATION of the SAS program for combination of yield, plant height, and plant circumference with forage yield. In addition, the yield components chosen as the independent variables were regressed with forage dry matter yield as the dependent variable.

Chapter IV

Results

4.1 Data over years

According to Bartlett's test of homogeneity the variances across years were significantly heterogenous. Thus differences were too large to permit the analysis of pooled data. Therefore each year was analyzed separately.

4.2 Dry matter yield

4.2.1 Swards

Orchardgrass dry matter yield in swards fluctuated significantly from cycle 0 to 3, but there were no significant differences between cycles in different years (Appendix 1). However, in Pennlate for two years there were increasing trends from cycle 1 to cycle 3. In Avon there was a decreasing trend from cycle 0 to cycle 3 in one year but it was not repeated in the other two years. In timothy, for both Salvo and Drummond, cycle 3 always had the highest numerical yield values but it was never significantly different from the other cycles (Figure 4.1, 4.2).

4.2.2 Spaced stands

Dry matter yields in orchardgrass did not respond significantly to selection across years and there were no consistent trends (Appendix 2, Figure 4.1). In Drummond timothy, for two years there were significant dry

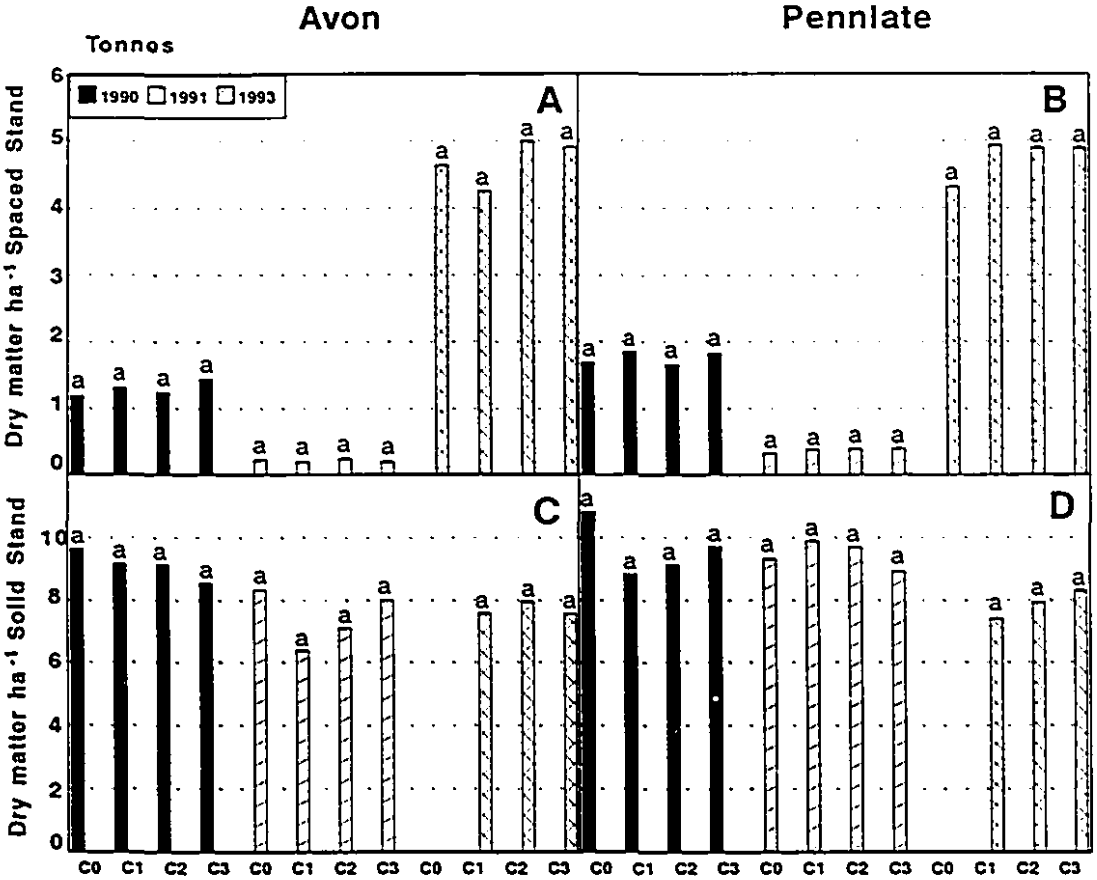

Figure 4.1. Comparison of dry matter yield in three cycles of recurrent selection in cultivars of orchardgrass in spaced and sward. A) Avon in three years in spaced stand. B) Pennlate in three years in spaced stand. C) Avon in three years in sward. D) Pennlate in three yearsin sward.
* Vaslues with the same letter are not significantly different.

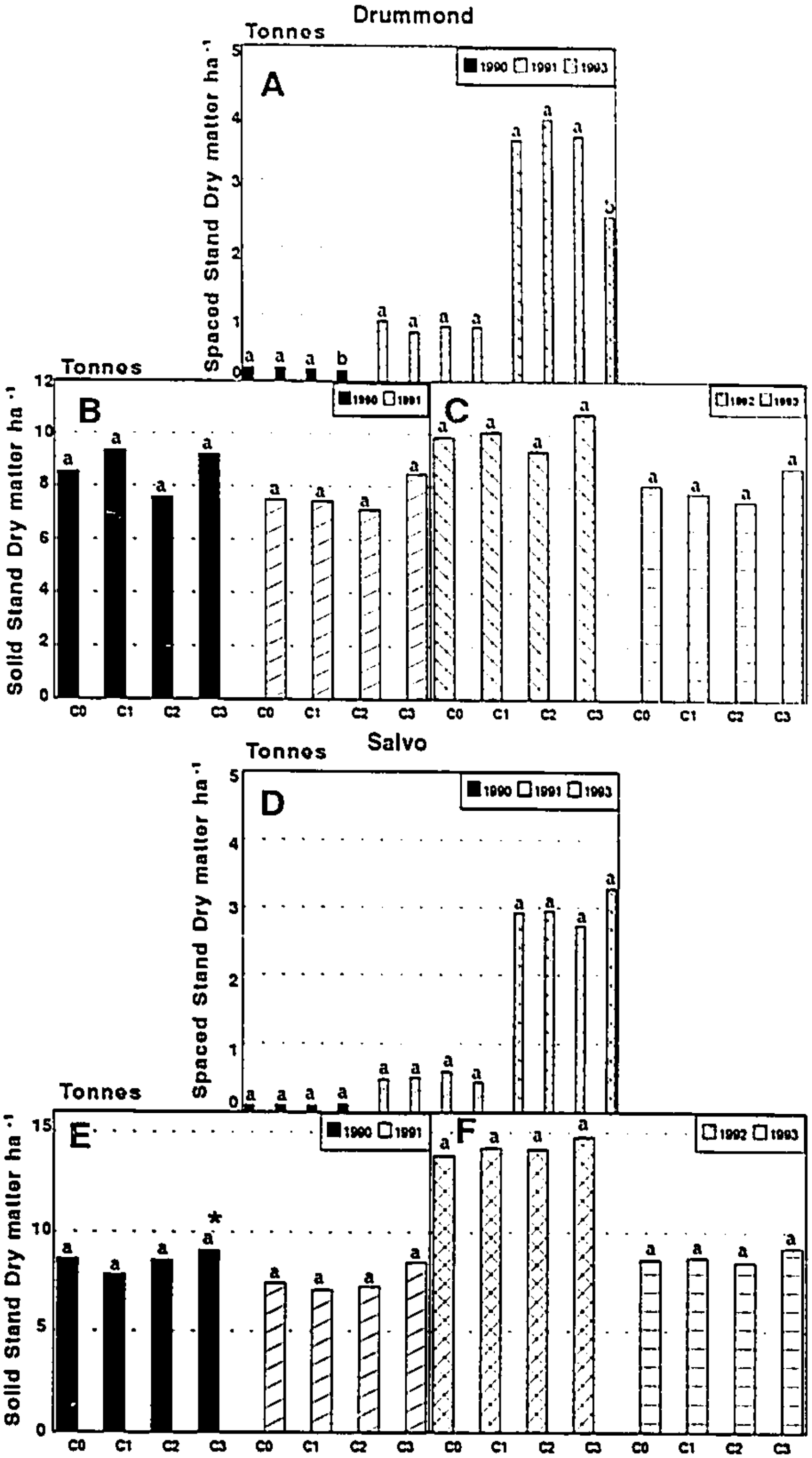

Figure 4.2 Comparison of dry matter yield of cultivars of timothy in spaced and sward. A) Drummond in spaced stand. B and C) Drummond in sward. D) Salvo in spaced stand. E and F) Salvo in sward.
* Values with the same letter are not significantly different.

matter yield (DMY) decreases for cycle 3 (Figure 4.2). For Salvo, neither significant differences nor consistent trends were found across cycles of selection (Figure 4.2).

4.3 Plant height

4.3.1 Swards

In 1993, there was a trend in Avon to increased height across cycles with cycle 3 being significantly taller (Table 4.1, Appendix.1). Cycles of Pennlate were not significantly different from each other (Appendix 1), but there was a trend for increasing height from cycle 1 to cycle 3 (Table 4.1). There were no significant differences, and no clear trends in height among cycles of the timothy cultivars.

4.3.2 Spaced stands

In Avon, there were no clear trends in height across cycles (Table 4.2; Appendix.3); however cycle 1 was significantly shorter than the other cycles in 1993. There were no significant differences among heights of cycles of Pennlate in any year; but, in all three years, the height of cycle 3 was numerically higher than the other cycles (Table 4.2).

For two years the height of cycle 3 of Drummond was significantly shorter than that of cycle 0 and the other cycles. Other than this, for all three years cycle 0 was numerically taller than the rest, suggesting apparent

Table 4.1. Plant height in four cycles of recurrent selection in cultivars of timothy and orchardgrass in solid stand in 1993

	Timothy		Orchardgrass	
	Drummond	Salvo	Pennlate	Avon
		Height (cm)		
Cycle 0	82.0 a*	86.3 a	---	---
Cycle 1	85.0 a	81.3 a	49.3 a	49.5 b
Cycle 2	81.3 a	83.3 a	51.0 a	53.3 b
Cycle 3	90.7 a	81.3 a	54.0 a	59.0 a

*Values with the same letter are not significantly different

Table 4.2. Comparison of varieties for plant height in timothy and orchardgrass in spaced stand in three years

	Timothy		Orchardgrass	
	Drummond	Salvo	Pennlate	Avon
		1990		
Cycle 0	87.0 a*	71.6 a	73.7 a	71.5 a
Cycle 1	85.8 a	67.3 b	79.2 a	72.6 a
Cycle 2	84.7 a	64.7 b	80.1 a	67.8 a
Cycle 3	77.5 b	65.7 b	82.1 a	70.8 a
		1991		
Cycle 0	70.8 a	83.5 a	84.6 a	69.9 a
Cycle 1	67.3 a	83.1 a	83.1 a	64.5 a
Cycle 2	69.9 a	85.0 a	82.5 a	67.6 a
Cycle 3	69.3 a	81.1 a	89.2 a	69.7 a
		1993		
Cycle 0	91.2 a	79.9 a	56.3 a	63.9 a
Cycle 1	90.7 a	82.7 a	61.0 a	57.0 b
Cycle 2	90.6 a	77.9 a	56.5 a	65.5 a
Cycle 3	86.8 b	70.6 a	61.8 a	68.0 a

*Values with the same letter are not significantly different tendency for reduced height in advanced cycles. For Salvo, in 1990, the selected cycles were significantly shorter than the original cultivar, while in 1991 and 1993, cycle 3 was numerically the shortest (Appendix 3; Table 4.2).

4.4 Plant circumference

Selection in Avon did not significantly change the plant circumference, but, cycle 3 always had the highest numerical value (Table 4.3). In the 1991 data, cycle 3 of Pennlate was significantly larger than the other cycles. Moreover, in 1990 all three selected cycles were numerically greater than the original cultivar (Appendix 4; Table 4.3).

In 1990, the circumferences of cycles 2 and 3 of Drummond were significantly reduced from cycles 0 and 1, while in 1993, cycle 3 had a considerably smaller circumference than the other cycles. Plant circumferences of Salvo were not significantly different over cycles (Appendix.4; Table 4.3).

4.5 Persistence

The number of surviving plants over cycles of Avon and Pennlate was not significantly different. However there was a tendency for better survival to be found in cycle 2 and 3 (Appendix 5; Table 4.4).

Plant persistence over cycles of Salvo was not significantly different in any year; but there was a trend to lower survival in selected populations. There was a significant decrease in cycle 2 of Drummond in 1990, but no significant response to selection was observed in the other years (Appendix 5; Table4.4).

4.6 Plant maturity

Maturity was measured only in 1993. Selection shifted advanced cycles of Avon toward later maturity with cycle 3 having a significantly later maturity, being approximately one day later than the other cycles (Table 4.5). The maturities of cycles of Pennlate were not significantly different (Appendix.7; Table 4.5). There was neither significant differences between cycles of Drummond nor a clear trend for number of days to reach the heading stage (Appendix.7; Table 4.5). There were no significant differences between cycles of Salvo; however, cycle 3 had numerically the latest maturity (Appendix.7; Table 4.5).

Table 4.3. Comparison of varieties for plant diameter in timothy and orchardgrass in spaced stand

	Timothy		Orchardgrass	
	Drummond	**Salvo**	**Pennlate**	**Avon**
		(cm)		
		1990		
Cycle0	62.1 a*	49.9 a	43.4 a	45.3 a
Cycle1	59.2 ac	49.6 a	51.2 a	44.2 a
Cycle2	54.8 c	47.5 a	50.6 a	44.6 a
Cycle3	55.2 bc	52.5 a	51.4 a	47.0 a
		1991		
Cycle0	57.4 a	47.7 a	50.7 b	46.7 a
Cycle1	55.4 a	50.5 a	50.7 b	46.7 a
Cycle2	58.4 a	53.3 a	51.9 b	48.6 a
Cycle3	57.0 a	49.9 a	60.4 a	48.1 a
		1993		
Cycle0	85.3 a	70.7 a	68.3 a	62.6 a
Cycle1	89.5 a	68.6 a	71.5 a	65.3 a
Cycle2	86.6 a	64.1 a	65.5 a	64.1 a
Cycle3	71.8 b	70.5 a	66.3 a	66.8 a

Table 4.4. Comparison of varieties for plant persistence timothy and orchardgrass in spaced stand

	Timothy		Orchardgrass	
	Drummond	Salvo	Pennlate	Avon
		1990		
Cycle 0	1.5708 a*	1.5708 a	1.3117 a	1.231 a**
Cycle 1	1.5708 a	1.5708 a	1.3599 a	1.170 a
Cycle 2	1.4501 b	1.5708 a	1.3567 a	1.360 a
Cycle 3	1.5708 a	1.5306 a	1.5708 a	1.188 a
		1991		
Cycle 0	1.5306 a	1.5708 a	1.243 a	0.979 a
Cycle 1	1.4904 a	1.5306 a	1.316 a	1.120 a
Cycle 2	1.5708 a	1.5306 a	1.312 a	1.104 a
Cycle 3	1.3922 a	1.4501 a	1.302 a	1.292 a
		1993		
Cycle 0	1.386 a	1.464 a	1.3090 a	1.090 a
Cycle 1	1.260 a	1.343 a	1.3626 a	0.891 a
Cycle 2	1.410 a	1.464 a	1.5172 a	1.369 a
Cycle 3	1.464 a	1.363 a	1.3433 a	1.202 a

*Arc-Sine transformed of the number of surviving plants
**Values with the same letter are not significantly different

Table 4.5. Comparisons of maturity of cultivars in timothy and orchardgrass in spaced stand in 1993

	Timothy		Orchardgrass	
	Drummond	Salvo	Pennlate	Avon
Cycle 0	79.3 a**	72.2 a	67.7 a	65.0 b*
Cycle 1	80.7 a	73.0 a	68.0 a	65.3 b
Cycle 2	78.7 a	72.7 a	67.0 a	65.3 b
Cycle 3	80.3 a	74.0 a	67.0 a	66.3 a

**Number of days from miminum temperature untile heading
*Values with the same letter are not significantly different

4.7 Seed yield

Seed yield was measured in 1993. In orchardgrass, no significant differences were found among cycles; however, in Avon, cycles 2 and 3 had numerically the highest yields, while, in Pennlate, cycle 3 had the lowest yield (Appendix 4; Table 4.6).

For Drummond there was a considerable reduction in seed yield in cycle 3. In Salvo, seed yields were very low, with cycle 3 being the highest, although it was not significantly different from the others (Appendix 4; Table 4.6).

4.8 Correlation

Correlation coefficients between dry matter yield of spaced stand and dry matter yield of the sward in orchardgrass ranged from -0.41 to 0.36 and were not significantly different from 0 (Table 4.7). In Drummond timothy, the correlation coefficients of the yield in different stands ranged from -0.03 to -0.14, and were not significant (Table 4.7). In Salvo timothy, the correlation coefficients of the yield in two kind of stands ranged from -0.22 to 0.55. They were not significant in 1990 and 1991 but in the last year (1993) a significant coefficient (r=0.55) was found (Table 4.7).

There were no significant correlations between heights of the two types of stands for the cutivars in this study. The correlation coefficients between seed yields and, respectively, plant height, plant circumference or forage dry matter yield in orchardgrass were non significant (Table 4.8).

4.9 Regressions

Coefficient of regression between forage yield and yield components showed that there were almost always significant effects of height and circumference on forage yield within both species (Appendix 6). In addition this effect was usually positive, i.g. the larger the height or circumference, the greater the yield (Table 4.9).

Table 4.6. Comparison of varieties for seed yield in orchardgrass and timothy in spaced stand in 1993

	Timothy		Orchardgrass	
	Drummond	Salvo	Pennlate	Avon
	kg ha $^{-1}$			
Cycle 0	562 a*	60 a	650 a	488 a
Cycle 1	600 a	55 a	610 a	478 a
Cycle 2	471.6 a	61 a	674 a	587 a
Cycle 3	238 b	71 a	430 a	545 a

* Values with the same letter are not significantly different

Table 4.7. Correlation between spaced-plant and solid stand in orchardgrass and timothy for dry matter yield, and height

	Dry Matter Yield			Height
	1990	1991	1993	1993
Timothy				
Drummond	-0.030	-0.222	-0.137	0.102
Salvo	0.263	-0.218	0.554 *	-0.256
Orchardgrass				
Avon	-0.409	0.360	-0.139	0.167
Pennlate	-0.053	-0.349	0.158	-0.016

* Significant at the 0.05% level of Probability.

Table 4.8. Correlation between seed yield and plant height, circumference, forage yield of orchardgrass

	Pennlate		
	Height	Circumference	Forage Yield
Seed Yield	0.1763	0.0762	0.1803
	Avon		
	Height	Circumference	Forage Yield
Seed Yield	0.0178	0.0633	-0.0023

Table 4.9. Regression equation between dry matter yield, height and circumference in orchardgrass and timothy

Species	1991	1993
Drummond	$Y = -674.0+9.8X+14.3Z$	$Y = -1233.6+21.8X+35.3Z$
Salvo	$Y = -648.4+6.7X+11.8Z$	$Y = -726.8+15.6X+33.6Z$
Pennlate	$Y = -37.8-1.1X+9.6Z$	$Y = -2051.3+53.8X+53.6Z$
Avon	$Y = -66.7+2.3X+2.7Z$	$Y = -307.8+48.7X+33.5Z$

Y = Dry Matter Yield (kg) X = Plant Height (cm)
Z = Plant Circumference (cm)

Chapter V

Discussion

According to the literature, direct selection for forage yield has been difficult and progress has been slow in all cool-season grasses. This can be partially explained by the nature of forage yield which is governed by polygenic systems and subject to environmental variation and genotype-environment interaction. Thus, the heritability of forage yield measured on individual plants may be expected to be low. Because of loss of families under selection, both population size and inbreeding depression may also be important elements (Burton, 1985b; Falconer 1981).

5.1 Orchardgrass

5.1.1 Sward

The separate analysis of data from these years (1990, 1991, 1993) showed that there was no statistically significant response to selection for dry matter yield. This lack of effectiveness could be explained in several ways: 1) The population size may have been too small. In comparison to Burton's (1985a) study, the population was smaller (400 plants) than that used for Pensacola bahiagrass (990 to 2200). The larger population size could have prevented inbreeding depression and controlled the loss of families and genetic drift through selection. This loss can narrow the genetic base and diversity of the population. Burton (1985a) pointed out that there are always a number of plants that fail to supply offspring to contribute to the next cycle in mass selection. However, in the present study, only cleaned seed was used to make sure viable seeds were being bulked from the selected plants. In the case of orchardgrass, because of decreasing trends realized in sward, it is possible that the base population (cycle 0) was not broad and diverse enough. 2) Selection in spaced planted nurseries was not effective in expressing sward yield (see discussion below). Overall, the yield results of the present study do not agree with the stepwise yield increase found under RRPS in Pensacola bahiagrass (warm-season grass) (Burton, 1985a).

The height of Pennlate and Avon showed a trend for taller stems, with cycle 3 in Avon being significantly taller. Despite the lack of yield increase, selection seems to have resulted in taller plant populations.

5.1.2 Spaced Stand

Since selections were carried out in a spaced stand, it would probably be more likely to find a response to selection in tests under those conditions. For yield, there was no significant response to selection, perhaps due to the reasons mentioned above. The relatively high coefficients of variation observed in the spaced stand evaluation experiments indicate that environmental variation can have a large effect on single-plant forage yield. Thus, low heritability of this trait during selection likely limited the response to selection.

The height of Avon and Pennlate did not significantly respond to selection. However, cycle 3 of Pennlate was always numerically higher, supporting the increasing height tendency seen above under swards. These results partially agree with those of Bowley et al., (1984) in which stem length of red clover increased in both spaced and sward under RRPS.

Avon showed a trend towards increasing circumference; there was a significant increase in circumference of Pennlate in one year and a positive trends towards greater circumference for the selected cycles. These results are in contrast with those of Bowley et al., (1984) in red clover in which selection for stem length was associated with a decline in stem number.

Plant persistence in Avon and Pennlate was not significantly changed under selection. However the tendency for better survival in advanced cycles was in contrast with that of Bowley et al., (1984) in red clover.

Pennlate did not show a significant change in maturity under selection. Nevertheless there was significant delay (approximately 1 day) in the time of heading in Avon under cycle 3. This is in agreement with the later maturity found in cycles of selection for yield in corn (Rodriguez et al., 1988).

There was no significant difference in seed yield among selected cycles of either Avon or Pennlate. Thus, selection for forage yield had no effect on seed yield. According to Burton (1974), the correlation coefficient between forage yield and seed head abundance was small and nonsignificant in Pensacola bahiagrass (the same nonsignificant correlation was found in this study). In contrast, Boe, and Ross (1991) found RRPS for high general combining ability (GCA) of seed retention in creeping foxtail could be achieved and at the same time parents which were capable of transmitting desirable height, as a component of forage yield, could be obtained.

5.1.3 Comparison of spaced and sward

With regards to the correlation of forage yields between spaced plant and sward (Table 4.2), there were no significant relationships in any year. The same was true for correlation of heights of the two stands. This may indicate the principal reason for the lack of response to selection found in swards. These results are in agreement with those of Nissen (1960), McElroy, and Christie, (1986) and Green and Eyles (1960); but in contrast to that of Burton (1985a).

5.2 Timothy

5.2.1 Sward

In four years of trials, significant response to selection was not found among cycles for dry matter yield. However, cycle 3 always had the highest numeric yield. The reasons for this lack of response may be similar to those mentioned above for orchardgrass. It is also possible that a larger member of replications in the evaluation trials would have permitted the detection of significant differences. However as the coefficients of variation in the present trials were acceptably low (Appendix. 1), increased replication probably would not have produced a significant increase in precision. Moreover correlation coefficients between spaced and sward were low (Table 4.7). These results are again in disagreement with those of Burton (1985a) for Pensacola bahiagrass, who found a good relationships of performance between the two stands.

Selection also had no significant effect on plant height. However, it is possible to select for different characters at the same time such as seed set and height in creeping foxtail. Applying RRPS, Boe, and Ross (1991) found that desirable heights of parents are accessible.

5.2.2 Spaced Stand

Dry matter yield was significantly lower in cycle 3 of Drummond in two of the three years, perhaps illustrating the effect of inbreeding depression. It is possible that the genetic base of this cultivar had been narrowed too much by three cycles of selection; however, there was no evidence of depression in swards. Salvo did not did not show this decline in yield.

Certain cycles of both Drummond and Salvo showed significant decreases in height and the overall trend was definitely towards reduced height over selection cycles. This correlates with the yield reduction in Drummond which is not surprising as height is a component of yield.

Plant circumference, another important yield component, declined in later cycles of Drummond in two of three years, but was not different among cycles within Salvo. Again this correlates well with the Drummond yield decline, suggesting inbreeding depression.

Winter survival of timothy over cycles showed a decreasing trend, moreover in one year, for Drummond, it significantly declined. These results agree with those of Bowley et al., (1984) in red clover, in which RPS for stem length decreased persistence of advanced cycles.

There was neither a significant nor clear trend in cultivars of timothy to the selection for number of days to reach the heading stage. In contrast, Rodriguez (1988) a found positive response to selection in corn yield was associated with taller plants, and later-maturing genotypes.

For Drummond, a large and significant reduction in seed yield was found for cycle 3. This may be explained by a reduction in plant circumference, thus, fewer stems. This is in contrast with that of Burton (1974), who has shown that the correlation between seed head abundance and forage yield was small and nonsignificant.

5.2.3 Comparison of spaced and sward

Generally correlations between spaced and sward stands for dry matter yields and plant height were low and non significant for varieties of timothy. However, in 1993 it was significant for Salvo. These results partially agree with those of Burton (1985a) in Pensacola bahiagrass. He found that well replicated spaced plant yields correlate well with seeded plot yields. In agreement to the non significant relationships found in the present study, McElroy and Christie (1986) and Nissen (1960), in timothy; and Green and Eyles (1960) in ryegrass found poor correlation between spaced and swards.

Chapter VI

6. General Discussion and Conclusions

Three cycles of recurrent restricted phenotypic selection (RRPS) were not effective in increasing the forage yield of two cultivars each of orchardgrass and timothy. Selection for improved yields in forage grasses has rarely resulted in much progress due to the complex inheritance of this trait. The lack of response in the present study may be explained by too narrow a genetic base in the source populations and by low heritability of single plant forage yield. In addition, the population size under selection may have been too small, resulting in inbreeding.

Elite, well adapted cultivars were used as the source populations in the present study. A more diverse population could have been produced by mixing several cultivars and introductions and this would have provided a wider genetic base for selection. The use of such a population may lead to progress from selection; however, the improved selection may still be inferior to elite cultivars. Thus in practical breeding terms, no progress would have been made.

Evidence for inbreeding was seen for space-planted Drummond timothy in the third cycle of selection. Forage and seed yields were reduced and plants were smaller in height and circumference. In swards, no reduction in these characters was seen for Drummond. In addition, no significant decreases were seen in any of the other three cultivars, suggesting that small population size may have been of lesser importance in the lack of response.

Another explanation for the ineffective selection may be the method of pollination used for the production of seed of each cycle. Selected plants were allowed to interpollinate in the field; however they were spread over the entire nursery, leading to a very non-random interpollination. In the RRPS programs of Burton (Burton, 1992), stem cuttings of selected plants were bunched for interpollination. This likely produces a more random pollination than in the present study. Seed production on cut stems is not possible in orchardgrass or timothy. It would be possible, however, to polycross selected plants in the greenhouse in the winter, providing sufficient facilities were available, or another possibility might be use of hydroponic culture in order to maintain flowering of selected stems and to provide sufficient nutrients for the seed setting stage. This would produce random interpollination and would provide seed for planting the next spring; thus no additional years would be required in each selection cycle. This would be a recommended improvement to the RRPS procedure for cool season perennial grasses.

The selection for forage yield carried out in this study produced some minor effects on certain other characters. There was a tendency towards increased plant height and circumference in orchardgrass. For timothy, however, height, and circumference were reduced by selection, particularly for Drummond. Cycle 3 of Avon orchardgrass was approximately one day later maturing than the unselected cultivar. There was also a tendency for similar later maturity for timothy.

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Appendix 1. Analysis of variance for orchardgrass and timothy for Yield and Height Solid Stand

Source variation	Mean Square			
	Timothy		Orchardgrass	
	Drummond	Salvo	Avon	Pennlate
	1990			
Block	980671	550316	2985950	5200633
Cycle	2551454	1040791	800292	1957919
Error	1840586	619680	2362657	831214
C.V.	16	9	17	10
	1991			
Block	3319549	267811	5813618	1886858
Cycle	1367690	1573583	1561188	829103
Error	873455	525655	1456288	2364360
C.V.	12	10	16	16
	1992			
Block	113962	2897583	—	—
Cycle	1350674	612146	—	—
Error	681763	1869996	—	—
C.V.	8	10	—	—
	1993			
Block	170167	509525	68972	93267
Cycle	1172550	399980	194850	814577
Error	398302	628505	240687	186734
C.V.	8	9	6	6
	Height (1993)			
Block	131	24	27	55
Cycle	75	22	92**	15
Error	62	150	11	10
C.V.	9	15	6	6

**significant at the 0.01 level of probability

Appendix 2. Analysis of variance for orchardgrass and timothy for yield in spaced stand in several years

Source of Variation	Mean Square			
	Timothy		Orchardgrass	
	Drummond	Salvo	Avon	Pennlate
		1990		
Block	7566	5458	4840126	10855450
Cycle	33985 **	3774	572332	795008
Block*Cycle	4418	1108	534237	1035383
Error	4470	1463	684199	872660
C.V.	36	37	64	53
		1991		
Block	1003912	231419	146035	690471
Cycle	365453	314317	40209	111094
Block*Cycle	162226	197401 **	59104**	123531**
Error	109052	54809	25396	47200
C.V.	40	47	72	56
		1993		
Block	4110455	1173375	5701337	5658572
Cycle	12409263**	1531083	3235031	2610760
Block*Cycle	1383903	596662	3460504 *	3594783
Error	1138381	816232	1696670	1672998
C.V.	32	30	28	27

** Significant at the 0.01 level of probability

Appendix 3. Analysis of Variance for Orchardgrass and timothy for plant height in spaced stand in several years

Source of variation	Mean Square			
	Timothy		Orchardgrass	
	Drummond	Salvo	Avon	Pennlate
	1990			
Block	353	316	6993	6402
Cycle	1470**	730**	275	1077
Block*Cycle	166	60	393	374
Error	161	98	556	439
C.V.	15	15	33	27
	1991			
Block	259	249	727	925
Cycle	182	208	539	510
Block*Cycle	107	287**	449	451
Error	129	128	346	352
C.V.	16	14	27	22
	1993			
Block	255	220	169	286
Cycle	795**	91	580**	182
Block*Cycle	156	96	274	308
Error	125	85	104	137
C.V.	14	14	16	20

**Significant at the 0.01 level of probability

Appendix 4. Analysis of variance for orchardgrass and timothy for plant diameter and seed yield in spaced stand in several years

Source of Variation	Mean Square			
	Timothy		Orchardgrass	
	Drummond	Salvo	Avon	Pennlate
	1990			
Block	219	400	3643	1262
Cycle	942 *	324	165	1098
Block*Cycle	199	176	231	657 **
Error	166	115	299	272
C.V.	22	22	34	34
	1991			
Block	211	71	662	1603
Cycle	119	415	58	1300 *
Block*Cycle	217 **	275 **	551 **	450 **
Error	100	122	233	226
C.V.	18	22	28	28
	1993			
Block	877	505	435	455
Cycle	1829 **	275	141	213
Block*Cycle	163	117	139	316
Error	287	193	144	142
C.V.	20	20	19	18
	Seed Yield			
Block	23413	433	19649	31291
Cycle	158287 **	273	17083	69905
Error	13666	257	8953	21687
C.V.	44	46	18	25

**Significant at the 0.01 level of probability

Appendix 5. Analysis of variance of plant persistence of timothy and orchardgrass in spaced stand

Source of Variation	Mean Square			
	Timothy		Orchardgrass	
	Drummond	Salvo	Pennlate	Avon
	1990			
Block	0.0069	0.0032	0.0691	0.1472
Cycles	0.0291**	0.0032	0.1079	0.0587
Error	0.0069	0.0032	0.0379	0.0566
C.V.	5	4	14	19
	1991			
Block	0.0117	0.0143	0.0786	0.1002
Cycles	0.0469	0.0205	0.0092	0.1323
Error	0.0207	0.0131	0.0613	0.0493
C.V.	10	8	19	20
	1993			
Block	0.0155	0.0216	0.1846	0.1833
Cycles	0.0448	0.0248	0.0509	0.2414
Error	0.0402	0.0524	0.0203	0.1376
C.V.	15	16	10	33

**Significant at the 0.01 level of probability

Appendix 6. Analysis of covariance between forage yield, height, and circumference in timothy and orchardgrass

Source of Variance	Mean Square			
	Timothy		Orchardgrass	
	Drummond	Salvo	Pennlate	Avon
		1990		
Model	---	168426 *	85941806 *	50660369 *
Height	---	39264 *	86339278 *	9718123 *
Diameter	---	138941 *	7414101 *	16771340 *
Error	---	494	561325	399867
C.V.	---	21	43	49
		1991		
Model	6952511 *	5161262 *	3177952 *	831955 *
Height	3658520 *	1757518 *	66704	263569 *
Diameter	6467717 *	5074541 *	4000409 *	246479 *
Error	91110	37952	46724	26044
C.V.	37	39	56	73
		1993		
Model	35311701 *	16494272 *	75671674 *	25193824 *
Height	6990318 *	2326277 *	41678098 *	27811178 *
Diameter	39444544 *	24139767 *	50820035 *	16309534 *
Error	997685	514921	647249	1043949
C.V.	29	24	17	20

*Significant at the 0.05 level of probability

Appendix 7. Analysis of variance for maturity in timothy and orchardgrass in spaced stand in 1993

Source of Variation	Mean Square			
	Timothy		Orchardgrass	
	Drummond	Salvo	Avon	Pennlate
Blocks	3.50	4.04	0.80	0.96
Cycles	5.05	3.60	2.0 *	1.50
Error	3.32	3.33	0.53	2.03
C.V.	2.3	2.5	1.1	2.1

*Significant at the 0.05 level of probability