NUTRITIVE VALUE AND PERENNIALITY OF PASTURE GRASSES

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Summary

In the genera *Phalaris* and *Lolium,* annual species have higher herbage nutritive value than perennials, and hybrids between annuals and perennials are intermediate. It is not yet known whether plant breeders will be able to improve the herbage quality of the perennial species without sacrificing some perenniality. Information needed to resolve this question could be obtained in various ways, some of which are discussed. Plant survival is of special importance in P. ***tuberosa,*** but in the ryegrasses some loss of perenniality has been tolerated by New Zealand farmers.

INTRODUCTION

THE COMPONENTS of herbage nutritive value responsible for animal productivity differences between grass species and cultivars are usually not clear. Problems of defining and predicting herbage quality have occupied ruminant nutrition workers for years (e.g., Ulyatt, 1970), and it is quite likely that the critical components vary with the species, the environment and the type of animal production. In many instances, herbage digestibility is the best single indicator of nutritive value. With the development of methods for measuring digestibility of small samples, especially the *in vitro* technique of Tilley and Terry (1963), plant breeders in Europe, North America and Australia have commenced breeding for herbage digestibility of temperate and tropical pasture grasses and legumes. From results so far obtained, it is clear that digestibility can be improved in most if not all species and that many other herbage quality weaknesses peculiar to individual species can be corrected.

The demonstration of genetic variability of herbage nutritive value in plant populations does not necessarily mean that improved quality can be obtained easily, or without changes in other important characters, or even that an improved variety will provide a pasture capable of higher animal production. Some of the complexities involved have been described (Clements 1969, 1970), but one aspect that has so far received little attention is the relationship between herbage nutritive value and perenniality.

A plant can be termed perennial if the balance between its rates of tiller production and tiller death is such that there are always some living tillers or tiller buds (L. T. Evans, 1964). For the purpose of this discussion, which will be restricted to temperate grasses, perenniality will refer to the ability of a plant to remain viable after the reproductive phase and to regularly survive the low moisture/high temperature stresses that occur during the summer. Each of these definitions permits a concept of relative perenniality, referring to the comparative abilities of species or cultivars to survive in any given environment. Thus in areas with very hot, dry summers the factors involved in perenniality (such as dormancy) may well be different from those factors important in milder areas. Similarly, a species or cultivar which is perennial in one environment may behave as an annual in another.

Phalaris and *Lolium* are very suitable genera in which to study the relationship between herbage nutritive value and perenniality. Each has well-defined annual and perennial members and a range of perenniality in the perennial members. In each genus, hybrids between annuals and perennials are available for study. Because they contain some of the agronomically most useful temperate pasture grasses, each genus has received considerable attention from plant scientists, so 'that new information can be considered in relation to existing knowledge.

RELATIONSHIPS IN THE GENUS *PHALARIS*

A wide range of Phalaris species together with several hybrids has recently been examined for herbage nutritive value and perenniality at: Palmerston North. The strains were grown as spaced plants (60 X 60 cm) in 1968 and were sampled as they reached the head emergence stage. Only tillers at this well-defined growth stage were taken, and an equal number were taken from each of eight plants of each strain in each of the three replicates. Harvested material was dried at 80° C, ground in an Apex cutter mill to pass through a 1 mm screen and analyzed for Kjeldahl nitrogen content and for in vitro digestibility (Tilley and Terry, 1963). The mean values for the species and hybrids, together with other relevant data are listed in Table 1. In Table 2, values for 8 strains of P. *tuberosa* (perennial), 6 of P. minor (annual) and 2 of P. *tuberosa* X ***minor*** (annual or weakly perennial) are presented. Further details of this equipment will be published elsewhere.

TABLE 1

Variation between Six Annual and Five Perennial ***Phalaris*** species, and Four Categories of Species Hybrids, for ***in vitro*** Digestibility and Nitrogen Content of Tillers with Heads Emerged.

Species *	No. Strains Examined †	Somatic Chromosome No.	Breeding System	Habit (ann. or per.) at Palm. Nth.	Species-Mean Values ± S.E. *in vitro* DOM (%)	*N* Content % of D.M.	Heading Date (Days after Oct. 1)
P. brachystachys	2	12	self-pollin.	annual	75.1 ± 0.3	1.34 ± 0.08	32.6 ± 0.2
P. minor	6	28	self-pollin.	annual	74.4 ± 0.6	1.81 ± 0.03	14.7 ± 0.5
P. amethystina	1	14	self-pollin.	annual	74.1 ± 1.7	1.24 ± 0.05	20.9 ± 0.1
P. caroliniana	1	14	self-pollin.	annual	72.6 ± 1.7	1.54 ± 0.06	32.4 ± 0.1
P. *californica*	1	28	self-pollin.	perennial	68.9 ± 1.7	2.08 ± 0.17	34.6 ± 1.0
P. *canariensis*	2	12	self-pollin.	annual	68.7 ± 1:7	0.91 ± 0.05	59.8 ± 0.5
P. *paradoxa*	2	14	self-pollin.	annual	67.1 ± 1.3	0.76 ± 0.04	53.1 ± 0.7
P. *truncata*	2	12	cross-pollin.	perennial	66.4 ± 1.8	1.35 ± 0.15	61.0 ± 1.7
P. coerulescens	5	14	cross-pollin.	perennial	65.8 ± 1.2	1.60 ± 0.02	48.5 ± 0.3
P. *tuberosa*	8	28	cross-pollin.	perennial	64.4 ± 0.4	1.38 ± 0.02	61.9 ± 0.2
P. arundinhcea	2	42	cross-pollin.	perennial	58.6 ± 0.5	1.58 ± 0.03	77.1 ± 0.7
P. brachystachys × minor ‡	1	40	self-pollin.	annual	76.7 ± 0.5	0.91 ± 0.07	40.5 ± 0.1
P. *tuberosa* × ***minor***	2	56	mainly self	ann./weak per.	70.2 ± 1.8	1.38 ± 0.02	45.6 ± 0.4
P. *tuberosa* × canariensis	3	40 (c.28)	mainly self	perennial	66.1 ± 0.4	1.32 ± 0.01	62.0 ± 0.1
P. *tuberosa* × orundinoceo	1	70	cross-pollin.	perennial	58.5 ± 2.7	1.45 ± 0.07	71.3 ± 0.8

* 6 of the hybrids are fertile allopolyploids. ***The*** exception, ***P. (tuberosa × canariensis) × tuberosa,*** is a fertile backcross hybrid with a somatic chromosome number of about 28.

† "Strains" include cultivars, ecotypes and experimental lines.

‡ This previously unreported hybrid was developed by Dr R. N. Oram, CSIRO, Canberra, Australia.

TABLE 2

Variation among strains of *P. tuberosa* and *P.* minor and Two Species Hybrids for *in vitro* Digestibility and Nitrogen Content of Tillers with Heads Emerged.

Species and strain*	Origin	in vitro DOM (%) ± S.E.	Nitrogen Content, % of dry matter ± S.E.	Heading Date (days after Oct. 1) ± S.E.
P. minor				
19215	Morocco	76.9 ± 1.0	1.28 ± 0.14	22.8 ± 1.42
19197	Egypt	75.8 ± 0.5	2.54 ± 0.25	-2.8 ± 0.8
19195	Libya	74.4 ± 0.9	2.11 ± 0.07	5.5 ± 0.7
19224	Greece	73.8 ± 1.5	1.07 ± 0.07	38.8 ± 0.4
32270	India	73.7 ± 1.7	1.90 ± 0.14	10.1 ± 0.7
32269	India	71.9 ± 1.4	1.98 ± 0.08	13.9 ± 0.8
P. tuberosa				
19280	Algeria	67.7 ± 0.4	1.55 ± 0.06	52.7 ± 0.8
Seedmaster	note (1)	66.4 ± 2.3	1.43 ± 0.01	68.8 ± 0.3
General Select	note (2)	65.4 ± 1.7	1.43 ± 0.01	63.1 ± 0.5
19315	Morocco	65.1 ± 1.7	1.42 ± 0.07	61.2 ± 1.1
High N	note (3)	64.8 ± 0.2	1.55 ± 0.07	59.6 ± 1.5
Low N	note (3)	63.7 ± 1.5	1.15 ± 0.00	56.2 ± 0.2
19351	Greece	61.4 ± 1.9	1.18 ± 0.02	80.0 ± 0.5
19305	Morocco	61.0 ± 1.7	1.37 ± 0.10	53.7 ± 1.4
P. tuborosa × minor				
cv. Australian x 19203	Italy (?) X Algeria	68.3 ± 2.3	1.12 ± 0.07	50.6 ± 1.0
"P. daviesii"	note (4)	72.0 ± 1.4	1.64 ± 0.08	40.5 ± 0.5

* Numbers used are CSIRO Commonwealth Plant Introduction (CPI) accession numbers.

(1) Improved cuitivar (McWilliam and Schroeder, 1965).

(2) Breeding population (McWilliam and Latter, 1970).

(3) Experimental selection lines derived from General Select (Clements, 1969).

(4) see Hutton (1955) and Blake (1956).

The main results are:

(1) As a group, annuals were earlier-maturing and had herbage of higher digestibility than perennials. After adjusting values to a common heading date (data not presented), annuals were still superior.

(2) There was significant variation independent of this simple classification. For example, herbage of P.

canariensis and P. *paradoxa* was less digestible than that of other annuals, while P. arundinacea had lower herbage digestibility than the other perennials. P. *californica* herbage was significantly more digestible than that of most P. *tuberosa* strains.

(3) With some exceptions, the hybrids were intermediate between their parent species for herbage digestibility and protein content. Digestibility in the hybrids was closely, and negatively, related to perenniality.

(4) As a group, the *P. tuberosa X* minor hybrids were significantly more digestible than *P. tuberosa* and less digestible than *P. minor*. The best hybrid was more digestible than any individual P. *tuberosa* strain.

(5) There was significant variation for herbage nutritive value within P. *tuberosa* and P. minor, suggesting that it may be possible to produce hybrids with higher herbage quality than those examined.

(6) P. *tuberosa* ecotypes often vary in summer dormancy (Hoen, 1968; Sankary et al., 1969), and there was considerable variation among the eight strains used in this experiment. There was no apparent relationship between the degree of summer dormancy and herbage nutritive value of the strains, a result which is supported by other work (Clements et *al.*, 1970). However, when three of the P. minor strains used in the experiment (19197, 19215 and 19224) were grown in a glasshouse, the least digestible strain was found to have a degree of perenniality, although in the field it behaved strictly as an annual.

RELATIONSHIPS IN THE GENUS *LOLIUM*

A similar broad relationship between herbage nutritive value and perenniality occurs in the genus *Lolium*. Butler et *al* (1968) have summarized several experiments which demonstrate differences between ryegrass varieties in ability to promote liveweight gains in sheep. In decreasing value, and increasing perenniality, the commercial cultivars are *L. multiflorum* (annual); *L.* perenne x multiflorum; *L. perenne* × *(perenne* X *multiflorum)* and *L. perenne* (perennial) . The ranking is consistent over many years and several sites, and the cultivars also rank in the same order in their ability to sustain milk yield in dairy cattle during the spring season (Wilson, 1967). Because they rank in the opposite order for milk butterfat content, the varieties do not always differ in ability to promote butterfat yield, while in the autumn, surprisingly, the effects on dairy cattle performance seem to be completely reversed.

These varietal effects are not due to differences in yield of herbage, but to some aspect of herbage nutritive value. Animal productivity differences are positively correlated with the ratio of propionic plus butyric to acetic acids in the rumen (Le., to the efficiency of utilization of digested energy and protein); with herbage intake and rate of passage of ingested herbage from the rumen, although these aspects have received relatively little attention; and, in some cases, with small differences in herbage digestibility. The varieties differ very little in gross chemical composition, including total carbohydrate content, except that perenniality is associated with a decrease in the ratio of soluble to insoluble carbohydrates. It is interesting that tetraploid strains of Lolium have higher ratios than comparable diploids (Dent and Aldrich, 1963; Alder, 1964; Davies, 1965; Wilson and Dolby, 1967), and that their herbage is usually more digestible (Alder, 1964; Green *et* al., 1965; Harkess, 1966; Wilson and Dolby, 1967). Cattle fed on herbage from tetraploid varieties may gain weight more rapidly (Alder, 1964) but milk yields are no higher and milk butterfat content may be less (Wilson and Dolby, 1967). Tetraploid strains of perennial ryegrass are reputed to be less per-. sistent.

DISCUSSION

It could be assumed from these results that breeding for some components of herbage nutritive value would result in a decrease in perenniality. However, the data do not provide any critical evidence in support of this view. It is clear that annual species of ***Phalaris*** and ***Lolium*** have higher herbage nutritive value than perennials, and that hybrids are usually intermediate both for nutritive value and perenniality. On the other hand, there is no proof that annuals are more nutritious because they are annuals. This is an important distinction. The evidence needed to resolve the issue could be provided in either of two ways.

First, plant breeders and geneticists could examine the genetic relationships between the two characters. This could be done, for example, by simultaneously selecting for perenniality and some chosen criterion of herbage nutritive value. A relationship due to linkage could be broken in this way, at least in the diploid ***Lolium*** species complex and probably in Phalaris tuberosa. If intense selection did not separate the characters, the association could probably be assumed to be due to very tight linkage or to pleiotropy. This sort of experiment, could provide a practical answer to the problem. In addition, the well-developed techniques of quantitative genetic analysis could contribute some useful information. Either approach should only be used on a suitable breeding population.

Some relevant data from plant breeding experiments are already available. In *Phalaris tuberosa,* it has been possible to produce selected lines which differ markedly in protein and soluble carbohydrate contents, but which do not appear to differ in perenniality at Palmerston North. In another experiment, full-sib families derived from P. *tuberosa* strain CPI 19280 showed wide variation in herbage digestibility, but all families appeared to be perennial at Palmerston North, Herbage from the best family was as digestible as that from one of the *P. tuberosa* × *minor* hybrids. A third piece of evidence in *Phalaris* is the existence of extensive strain variation within the perennial species P. *tuberosa* (Table 2). In the case of Lolium, Wilson (1965) has selected for high and low cellulose content within *L.* perertne X *(perenne* X *multiflorum)*, and these selected lines do not noticeably differ in perenniality under spaced-plant conditions at Palmerston North. In addition, Barclay (1967) has produced a tetraploid strain of the same ryegrass cultivar which may have lower cellulose content than the commercial diploid strain, but which seems to be similar in perenniality (P. C. Barclay, pers. comm.).

The second potential source of critical information is the plant physiologist/biochemist. It is likely that herbage nutritive value can be related to biochemical processes. which result in certain features of morphology, anatomy and chemical composition. The question is, are these same processes or features concerned with perenniality?

Again, some information is already available. In Lolium, it can be deduced from the results already outlined, together with data on the relative anatomy and morphology of ryegrass varieties (P. S. Evans, 1964, 1967; Sant, 1969) that the ratio of soluble to insoluble carbohydrates partly depends on the ratio of cell cytoplasm to cell wall, and that this in turn may be a function of cell size. It is easy to suggest ways in which each of these characters might be related to the perennial response. However, the exact natures of the relationships, if they exist, are not yet clear. If, as L. T. Evans et al. (1964) have suggested, the growth patterns of temperate grasses reflect a hierarchy of sinks for photosynthetic products (e.g., soluble carbohydrates), then differences in soluble carbohydrate concentration or movement within the plant may partly control the length of the life cycle. For example, is perenniality, like cell size, partly a function of the relative sink strengths of inflorescences, tiller buds and roots? McWilliam (1968b) has shown that photosynthate accumulates in the tubers of P. *tuberosa* and provides a store of energy for the dormant tiller buds, while in P. *minor* there is no such accumulation. The patterns of translocation of photosynthetic products after anthesis are different in the two species, which suggests that competitive abilities of the various meristems for substrate differ between the species. The question remains, however, whether the carbohydrate accumulates in *P. tuberosa* tubers because the roots and tiller buds stay alive, or whether the change in translocation pattern which occurs after anthesis allows the roots and tiller buds to remain alive. This is a critical question. Death of the root system of the annual, which is anatomically and morphologically different from that of the perennial (McWilliam and Kramer, 1968) would drastically reduce the ability of the roots and tiller buds to compete for photosynthate and would consequently alter translocation patterns, Although some storage tissue and stored carbohydrate are necessary to ensure survival of a dormant *P. tuberosa* plant or tiller bud (McKell et *al.*, 1966, 1970; Berry and Hoveland, 1969), the critical amount is not known, and in arid areas survival of a dormant bud depends at least as much on its moisture supply as its energy supply (McWilliam and Kramer, 1968).

Another character which is negatively related to herbage digestibility differences among *Phalaris* species (Table 1) and sometimes within plant populations of other species is maturity time, as measured by date of ear emergence. L. T. Evans (1964) has suggested that perenniality in sparse flowering temperate grasses may be partly due to their long vernalization requirements. However, in *P. tuberosa* where time to maturity closely reflects vernalization requirement (Cooper and McWilliam, 1966), there is actually a negative phenotypic reiationship between maturity time and plant survival in severe Mediterranean climates (Hoen, 1968). In this species there is usually no marked phenotypic relationship between heading date and *in vitro* digestibility (Table 2; Clements et al., 1970), while genetic relationships differ according to plant populations and growth stages (unpublished data). An examination of the relative perenniality and herbage quality of McWilliam's (1968a) lines selected for high and low vernalization requirement would provide interesting information. The relationship between nutritive value and heading data will be described in a separate publication.

The possibility that some underlying physiological processes are common to both herbage quality and perenniality will remain uncertain until more is known of the physiology of each character. Although plant breeders may be able to separate the two traits, this does not lessen the importance of understanding basic processes in plants.

CONCLUSIONS

The results described here are provocative in that, though they do not provide conclusive evidence, they suggest that some important aspects of herbage nutritive value are closely associated with the annual habit. If this is true, what compromise (if any) will be necessary in plant breeding programmes? Recently, the need for perenniality in pasture grasses has been questioned (e.g., Axelsen and Morley, 1968; Reed, 1970). However the strong perenniality of *P. tuberosa* determines its persistence in pastures, and will remain a critical characteristic until varieties are produced which can re-establish from seeds falling on the soil surface. On *the* other hand, *tyegrass is* relatively easy to establish, and the perenniality and persistence of normally short-lived types can be increased at some expense by grazing management (e.g., Brougham, 1961; Harris, 1970). For these reasons, and despite substantial plant mortality that will occur during summer drought conditions, a degree of perenniality can be sacrificed for the superior productivity and herbage nutritive value of the hybrid cultivars. That this is so is suggested by the extensive use of the annual and short-rotation ryegrasses in New Zealand.

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DISCUSSION

To a suggestion by Bailey that there might be quicker methods of measuring perenniality rather than just waiting to see if a plant grows for several years or not, Clements said that perenniality was a relative phenomenon varying with environment and was thus hard to define. He had no knowledge of a quick test, but a more complete understanding of the physiology of the plant might help. Langer thought the proportion of flowering or non-flowering tillers might assist.

Wedin (U.S.A.) said he was confused as to exactly what was meant by a perennial. Clements said it would be the ability of a species to maintain viable tillers indefinitely, but it was a function of the environment. For instance, a plant might be a perennial in Palmerston North but an annual in Canberra. Evans had suggested that perenniality could be closely correlated with vernalization.

To an inquiry from Marten (U.S.A.) as to whether *Phalaris* arundinacen was one of the poorest grasses, Clements said that he had no data except that it had always baen less digestible. He considered that P. *tuberosa* had roughly the same nutritive value as cocksfoot, but not as high as that of ryegrass.

Woodford (U.K.) commented that in comparing annuals and perennials one had to be very careful to select a stage of growth that was comparable. Clements had picked heading which seemed to him to be the worst possible stage. He was interested to know what would have happened had the comparisons been made at the vegetative stage of growth. Clements said he had avoided bias by sampling only tillers at the required stage of growth. It was very difficult to choose a meaningful growth stage. At other stages of growth, results might have been different.

Concerning nutritive value and perenniality, Clements said only now was an endeavour being made at Palmerston North to select for both. Previously it had been for yield and perenniality. He himself had found a negative correlation between heading date and nutritive value.