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Vegetative tiller allometry and biomass relations in a field population of *Festuca rubra* s. s.

Vztah mezi biomasou a allometrií vegetativních odnoží v přírodní populaci *Festuca rubra* s. s.

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Five linear measures (length of the longest leaf blade, length of the youngest fully developed leaf blade, length of the longest living sheath, diameter of the sheath, diameter of the youngest leaf blade) and number of leaves were used to predict the tiller dry mass. Length of the sheath, length of the leaf and sheath diameter were the best single predictors. All the variables considered accounted for 86.1% of the variance in tiller mass. The prediction using number of leaves and length of the longest leaf still amounted to 64.2% of the variance in tiller mass. There are differences in allometric relations between populations.

Introduction

Plant aboveground interference is strongly correlated with the size of the plant individual; the effect of size is generally much more important than the effect of the species identity (Goldberg et Werner 1983). Though there is a considerable amount of theory concerning the role of plant size in the development of plant stands (e.g. Weiner 1985, Weiner et Solbrig 1984, Hara 1988), its measurement is often arbitrary. Generally the biomass of the plant individual or module is assumed to be the best expression of its size; since the direct measurement of the biomass is inherently destructive, alternative approaches have to be sought for repeated observations during one experiment. Such an approach exploits correlations between linear measures of plant size and plant mass.

Tillers in grasses are in many respects difficult to compare to individuals of dicot herbs (let alone trees). They were shown to play a similar role as leaves in dicots (Sydes 1984) and their size therefore might be of lesser ecological interest. Still, studies dealing with the finer processes in the grass tussocks cannot avoid the estimation of tiller size. Many studies tacitly assume tillers as being equivalent in their size (e.g. Fetcher et Shaver 1983, Butler et Briske 1988 and many others), but explicit studies on the subject are rare (Colvill et Marshall 1984). The present paper aims to find easily measurable predictors of the tiller mass in field growing populations of *Festuca rubra*.

Methods

Festuca rubra tussocks were sampled in September 1985 in two managed grasslands in the Krkonoše Mountains, North Bohemia (Czech Republic). One locality was a species rich grassland (Janovy boudy, 3.75 km ESE of the Pec pod Sněžkou settlement, 50° 41' 28" N, 15° 47' 35" E, altitude 880 m a.s.l.) and the other a species poor grassland (Severka settlement, ca. 3 km NW of Pec pod Sněžkou, 50° 41' 42" N, 15° 42' 25" E, altitude approx. 1100 m a.s.l.). Both localities can be classified as *Sileno-Nardetum* (*Nardo-Agrostion*, *Nardetalia*); the species rich one as subassociation *crepidetosum* and the species poor one as subassociation *pleurozietosum* (Krahulec 1990). Traditionally, the grasslands were mowed once or twice a year (depending on the weather) and grazed late in autumn. They were manured once in several years.

One large loose tussock was selected at each locality. These tussocks were removed from the soil and individual tillers were separated. Roots and attached rhizome were separated and the sheaths of dead leaves were removed. All tillers were measured except those obviously damaged. Thirty three tillers were measured at the first locality, fifty at the second locality.

Five linear measures, the number of leaves and the dry mass were obtained for each tiller (Table 1). Length variables (LENBLADE, LENYOUNG, LENSHEATH) were measured to the nearest millimeter, diameter variables (DIAMSHEATH, DIAMBLADE) to the nearest 0.1 mm (using a measuring lens), and tiller dry mass was measured to the nearest milligram.

Results

All linear measures were strongly intercorrelated. The correlations of untransformed variables were in all cases higher than the correlations of log transformed variables; within the measured range there is no unequivocal indication of an allometric relation between the variables. The untransformed values were used for further analysis.

The first PCA axis of the linear variables (LENBLADE, LENYOUNG, LENSHEATH, DIAMSHEATH, DIAMBLADE) accounted for 75% of their total variance; the first two

Table 1. - Variables recorded for each tiller

Name	Definition
NOLEAF	Total number of green leaves. All exserted leaves with at least 50% blade length green were counted.
LENBLADE	Length of the longest leaf blade
LENYOUNG	Length of the youngest fully developed leaf blade (i.e. with visible sheath)
LENSHEATH	Length of the longest living sheath (usually sheath of the youngest leaf)
DIAMSHEATH	Diameter of the sheath, measured at the middle part of the sheath of the youngest leaf
DIAMBLADE	Diameter of the youngest leaf blade, measured in the middle part of the folded blade
MASS	Tiller dry mass (dried to constant weight at 80°C)

axes accounted together for 87% of the total variance. The first PCA axis summarizes the overall size component of the length variables; all these variables had a high loading on the first axis (Fig. 1). The second axis separates clearly the length variables (LENBLADE, LENYOUNG, LENSHEATH) from the diameter variables (DIAMSHEATH, DIAMBLADE) and thus expresses a measure of the length/width ratio of tillers.

The number of leaves was very poorly correlated with the length variables. Its squared correlation coefficient with all five of them was only 0.247; the squared correlation coefficient of each linear measure with the rest of the linear variables ranged from 0.68 to 0.82. Consequently, the correlation coefficient of the number of leaves with the axes of PCA of the linear variables was very low and nonsignificant (r = -0.118 for axis 1, r = 0.164 for axis 2).

Tiller mass was predicted very well by the other size variables of a tiller (Tab. 2, 3, Fig. 2). The highest correlation was shown by the sheath dimensions (both length and diameter), though the differences are slight. Tiller mass was well correlated with the first PCA axis of the length variables (r = 0.889, P<0.001), whereas it was not correlated with the second axis (r = 0.101 n.s.). Surprisingly, the number of leaves was very poorly correlated with the tiller mass; though, owing to virtual absence of correlation with the

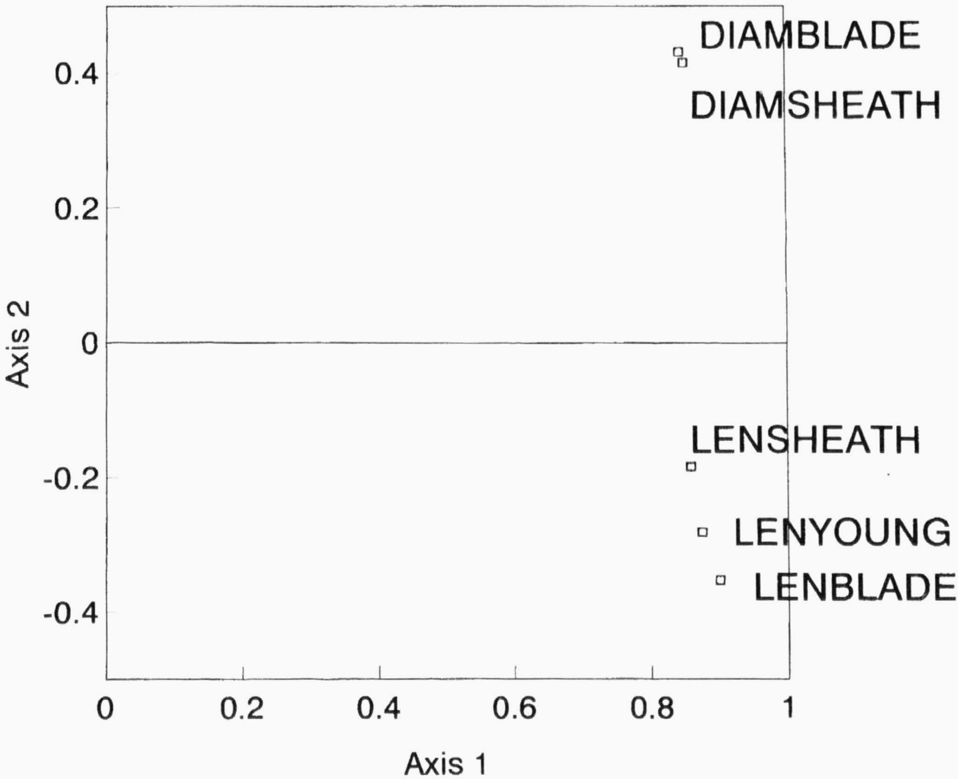

Fig. 1. - PCA loadings of the length variables. See Table 1 for explanations of the variables names.

length variables, it adds another component for the tiller mass prediction. The predictive power of individual combinations of variables which could be used for routine prediction always exceeded 60% of the variance in mass (Table 3).

More detailed analysis shows that there are differences in size relations between tillers from individual tussocks (and localities). Analysis of covariance demonstrated that the slope of the relation between mass and length variables differed between groups (Table 4). The slopes in the tussock from the first locality (species rich) were invariably lower than those from the second locality (species poor). Also the overall correlation within the set of linear variables was less in the tussock from the first locality than in that from the second one: the first PCA axis of the length variables accounted respectively for 41.6 and 76.5% in the first and second tussocks, whereas the second PCA axis accounted for 32.6 and 11.7%. This indicates much higher colinearity of all size variables in the tussock from the second locality. Still the pattern of loadings of both axes (the size component vs. length/width ratio) does not differ between the tussocks.

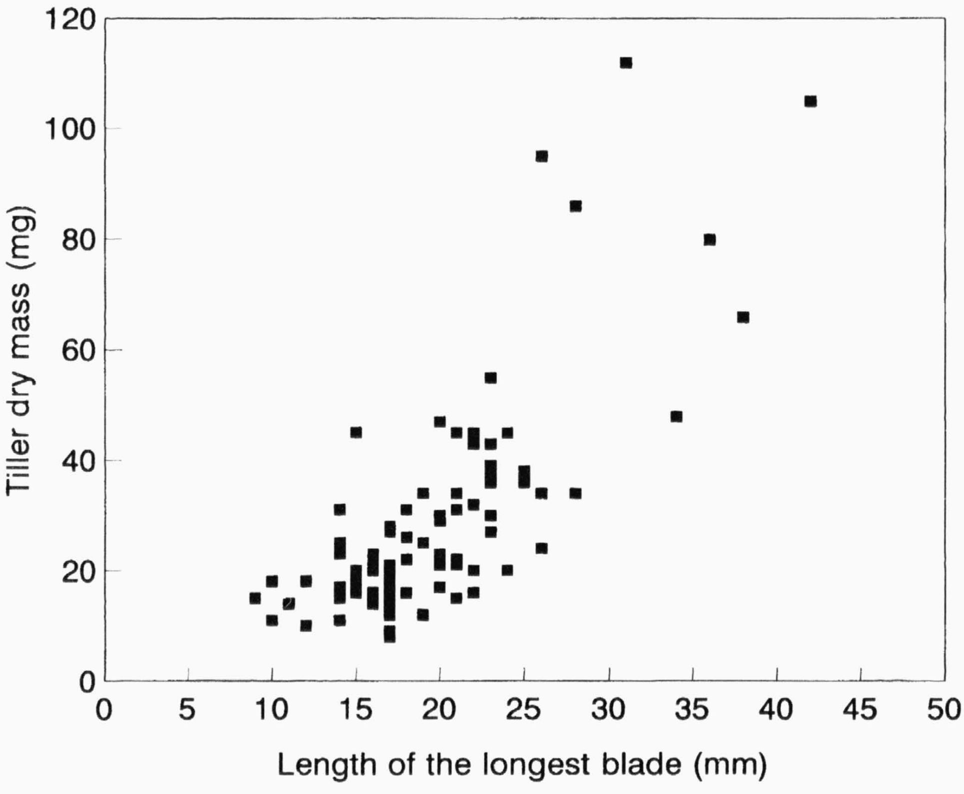

Fig. 2. - Relationship between the length of the longest leaf and the tiller mass (r^2=0.759).

Table 2. - Correlation of the tiller mass with the size variables (see Table 1 for definition of variables considered). Student's t-tests were applied for significance testing. n.s - nonsignificant.

Variable	Correlation coefficient	Significance (n=83)
NOLEAF	0.157	n.s.
LENBLADE	0.759	P<0.001
LENYOUNG	0.689	P<0.001
LENSHEATH	0.819	P<0.001
DIAMSHEATH	0.804	P<0.001
DIAMBLADE	0.778	P<0.001

Table 3. - Prediction of tiller mass by different sets of predictor variables

Variable set	Adjusted R^2
all	0.861
all without NOLEAF	0.815
all length variables + NOLEAF	0.762
all length variables	0.702
all leaf blade variables + NOLEAF	0.818
all leaf blade variables	0.727
all length leaf blade variables + NOLEAF	0.669
all length leaf blade variables	0.573
LENBLADE + NOLEAF	0.642
LENBLADE	0.572

Table 4. - Tests of equality of slopes in the regression of tiller mass on tiller size variables between localities (Analysis of covariance, d.f. 1, 80).

Variable	F-statistic	Significance
LENBLADE	9.28	P<0.01
LENYOUNG	21.39	P<0.001
LENSHEATH	11.27	P<0.01
DIAMSHEATH	4.98	P<0.05
DIAMBLADE	0.75	n.s.

Discussion

The results show that the prediction of the tiller mass by the employed predictor variables is satisfactory. Still routine employment of these correlations possess some difficulties. Though the single predictive power of LENSHEATH is the highest among the reported length variables, it cannot be used for routine measurement, since usually part of the sheath is hidden in the litter and its measurement would involve undue disturbance of the tussock. In a similar vein, the high predictive power of the diameter variables (DIAMSHEATH, DIAMBLADE) is also difficult to exploit in the field owing to the potentially destructive effects of magnifying glass measurement within the stand. The remaining variables (LENBLADE, NOLEAF and LENYOUNG) still accounted for a reasonable proportion of the total variation in biomass (Table 3). However, adding the leaf diameter to these three variables increased the predictive power considerably (further 15% of the total variance in biomass); inclusion of further variables would not improve significantly the predictive power of the regression equation.

Together with the LENSHEATH, the diameter variables are very good predictors of the tiller mass (Table 1). Importantly, this is not due to their separate effect on tiller „robustness“ or shape (Bookstein 1982). In contrast, this is due to their correlation with the overall size component of the tiller; the „shape“ component identified by the PCA and interpretable as length vs. diameter ratio is not correlated with the tiller mass.

In the present study, logtransformed variables were shown to be correlated less than untransformed variables, in spite of the rather wide range of values recorded. Though there could be nonlinearity in the plot of untransformed variables (Fig. 1), it cannot be proved using the present data set. The power curve correlation is generally interpreted in terms of the allometric growth, i.e. the constant ratio of growth rates between different parts (Gould 1979). However, the studied tiller population cannot be fully conceived as a population differing only in the growth status. The size differentiation in tillers may be due to many factors (competition, position within the stand, order etc.); all tillers then do not necessarily follow the same growth pattern.

The difference between both samples studied with respect to the slopes of the regression lines (and to the overall correlation strength) corresponds well with the published data on allometric relations in plants, which have been shown to depend on many stand parameters (Stanhill 1977, Joliffe et al. 1988). Owing to this specificity, the transfer of regression equations from study to study is not recommendable. Still the general pattern of correlation seems to be much less variable. There is a further complicating factor in *Festuca rubra*: this species is known to produce two types of tillers (intravaginal and extravaginal) which may be expected to obey different allometric relations. Unfortunately, these tiller types cannot be separated operationally in the field except at a very early stage.

Souhrn

V práci byl zjišťován vztah mezi allometrickými charakteristikami vegetativních odnoží *Festuca rubra* s. s. a jejich biomasou. Biomasa odnože byla predikována na základě pěti délkových proměnných (délka nejdelší čepele, délka nejmladší plně vyvinuté listové čepele, délka nejdelší živé pochvy, průměr pochvy, průměr nejmladší listové čepele) a počtu listů. Nejlepšími prediktory byly délka pochvy, délka listu a průměr pochvy. Pomocí všech prediktorů bylo vysvětleno 86.1% variability biomasy odnoží. I zahrnutím pouhého počtu listů a délky nejdelšího listu bylo vysvětleno 64.2% variability. Jednotlivé populace se navzájem liší v allometrických vztazích.

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