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The use of frequency estimates in studying sward structure

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Abstract

Estimates of the frequency of absence of rooted perennial ryegrass tiller bases from concentric sampling quadrats of different sizes are recommended for characterizing the open space structure of perennial ryegrass swards. It is proposed that these estimates are useful for evaluating the persistence of grass species and cultivars in swards. Data on this aspect of sward structure could provide criteria for the productivity of a sward and thus for the need to reseed grassland.

Introduction

The most widespread methods used to characterize sward composition are those which measure cover and population density (for definitions see Brown, 1954; Mitchell and Glenday, 1958; Greig-Smith, 1983). Some authors (e.g. Brown (1954) and Aberdeen (1954, 1958)) have discussed an alternative method for the analysis of botanical composition, based on frequency estimates of species in quadrats. However, according to Greig-Smith (1983) it is a serious drawback of these estimates that they depend on quadrat size, plant size and aggregation. This point was also recognized by Aberdeen (1954, 1958) who derived a relationship between absence frequency of species in concentric quadrats and plant density, plant size and quadrat size, for random distributions of plants of equal size. Although this drawback of presence frequency estimates in quadrats invalidates their use for assessing botanical composition, this does not mean that they cannot provide any useful information. It will be argued in this paper that, in a grass sward, if the presence of rooted tiller bases in concentric sampling quadrats of different sizes is recorded, then the calculated absence frequencies can provide valuable information on sward structure.

The absence frequency of rooted tiller bases from quadrats with radius R is the same as the frequency with which distances occur of at least R from observation points to nearest plants. Thus, the absence frequency from quadrats with radius R is equivalent to the proportion of the sward area in which the points are at a distance of at least R from nearest plants. Information on absence frequencies in quadrats of a certain critical size can be used in principle for calculating the total unproductive area of a sward, or the total area that is low yielding because of patches of species of low productivity.

In this paper, first the theoretical background of the relationship between absence frequency and quadrat size will be examined. It will be demonstrated which absence frequencies in relation to quadrat size can be expected for some different hypothetical spatial structures of grass swards. Second, some measured absence frequency curves of perennial ryegrass swards differing in aspects such as management, cultivar, age and plant density will be presented. These will be discussed in view of theoretical expectations. Third, absence frequencies of plants from quadrats will be related to measured grassland yields in order to determine whether absence frequencies can be used to assess the

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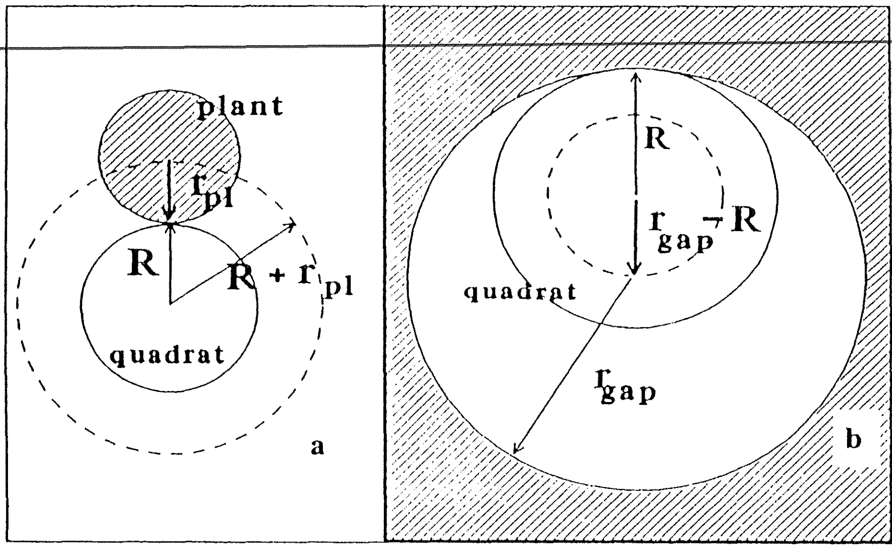

Figure 1. (a) Plants recorded as present in quadrats, if they only so much as touch the quadrat. R = quadrat radius; r_{pl} = plant radius. (b) A gap with radius r_{gap} will result in an 'empty' record for a sampling quadrat with radius R, when its centre falls within the dashed circle with radius ($r_{gap} - R$).

productivity of a sward. These relationships can be used to support reseeding decisions. This will be evaluated on the basis of recently published results by van Loo (1991). Finally, it will be shown that for an adequate description of spatial sward structure, the usual cover and population density estimates are not sufficient, and should be combined with absence frequency estimations.

Theoretical considerations

Equations

The relationship between absence frequency and quadrat size depends not only on the plant density and plant size but also on the spatial distribution of plants. Plant distribution is important because swards can be homogeneous with a more or less random plant distribution (as could be the case in newly sown grasslands), or heterogeneous, for instance because of open patches (gaps), caused by urine scorch. Swards can also become heterogeneous when damaging factors only result in patches with reduced plant density. The effects of gaps and of localized differences in plant density can be theoretically calculated. Calculations will be made for theoretical cases of sward damage by urine excretion. Urine excretions can have different effects on the sward, varying from total plant kill due to urine scorch, to only fractional decline in plant density or even no damage at all.

Absence frequencies of plants from quadrats can be calculated for given densities and sizes of randomly distributed plants using Aberdeen's equation (Aberdeen, 1954, 1958). When 'clumping' of individuals has to be taken into account, the negative binomial function (Bliss and Fisher, 1953; Petersen *et al.*, 1956) can be used. It will be shown below that with some adaptations Aberdeen's equation can also be used for calculating absence frequencies of plants from quadrats from given densities and sizes of gaps (urine scorch patches).

Plant density related absence frequency. In a population of plant individuals with no size (points), let z_{pl} be the mean number of plants per sampling quadrat. Then, in the case of a random plant distribution, the number of individuals per quadrat is Poisson distributed, and therefore the proportion of quadrats with no plants (absence frequency of plants from quadrats; a_{pl}) is:

$$a_{pl} = \exp(-z_{pl}) \quad (1)$$

z_{pl} depends on the density (d_{pl}) of individuals and the quadrat size, i.e. if R is the radius of a circular quadrat, then:

$$z_{pl} = \pi R^2 d_{pl} \quad (2)$$

Aberdeen (1954, 1958) considered the more realistic case where plants have appreciable dimensions, and where all plant individuals whose centre points are at a distance equal to or less than the plant radius r_{pl} from the circumference of the quadrat are recorded as present (Figure 1a). Since this is the same as recording the presence of plant individuals of point size in quadrats of radius $(R+r_{pl})$, z_{pl} may be calculated as:

$$z_{pl} = \pi (R + r_{pl})^2 \, d_{pl} \qquad (3)$$

Absence frequency due to gaps. When a quadrat falls completely within a gap it is empty. This is the case when the distance between the centre of the quadrat and the centre of a gap is less than $r_{gap} - R$ (Figure 1b). Thus, the probability of a quadrat falling completely within a gap is the probability of one or more centres of gaps being present in a circle with radius $r_{gap} - R$. This probability is the same as one minus the probability of no centres of gaps being present within a radius $r_{gap} - R$. When the gaps are randomly distributed the probability (f) of a quadrat falling completely within a gap is then:

$$f = 1 - \exp\,(-z_{gap'}) \qquad (4)$$

where

$$z_{gap'} = \pi (r_{gap} - R)^2 \, d_{gap} \qquad (5)$$

$z_{gap'}$ is the mean number of gap centres in circles with radius $r_{gap} - R$, and d_{gap} is gap density.

Compound absence frequency calculation. For a compound absence frequency calculation from given plant densities and plant size and given densities and sizes of gaps (urine scorch patches), for each quadrat size first the absence frequency outside the gaps, i.e. due to the plant density, is calculated as $a_{pl}\,(1-f)$. Accordingly, the total absence frequency (a_t) per sampling quadrat can be approximated by:

$$a_t = f + [a_{pl}\,(1-f)] \qquad (6)$$

Absence frequencies in cases of patches with different plant densities. For the case that urine excretions are assumed to cause only fractional declines in plant density, not only the total area proportion covered by urine patches but also the respective area proportions that have been covered once, twice and more times have to be calculated.

First, the average number of times (z_{ptch}) a point in the sward is covered by urine patches is calculated from:

$$z_{ptch} = \pi (r_{ptch})^2 \, d_{ptch} \qquad (7)$$

where r_{ptch} is radius of the patch, and d_{ptch} is patch density.

Next the respective area proportions covered i times $(i=0,1,2....k)$ are calculated from the general term of the Poisson progression:

$$p(i) = \frac{\exp(-z_{ptch})\, z_{ptch}}{i!} \qquad (0 \le p(i) \le 1) \qquad (8)$$

or, for the theoretical case of strong clustering of urine patches, from the negative binomial function according to:

$$p(i) = \frac{(k+i-1)!}{i!\,(k-1)!} \cdot \frac{U^i}{q^k} \qquad (9)$$

where $q = (k + z_{ptch})$; $U = z_{ptch}\,(k + z_{ptch})$, and k is a parameter measuring the non-uniformity of the distribution. A low k value simulates strong clustering.

Some calculations

All graphs in Figures 2a, b and c (theoretical cases of sward damage in urine patches) are calculated on the basis of the following same assumptions for an intensively used perennial ryegrass sward: a plant density of 3 plants dm^{-2} and a mean plant radius at that density of 1 cm; 7 grazing periods of 4 days per year; a stocking rate of 30 cows ha^{-1}; 13·5 urine excretions per cow per day and an average urine patch size of 65 dm^2. Three plants dm^{-2} corresponds with the maximal density found by Kreuz (1969) after two years of self-thinning in a plant density experiment with perennial ryegrass at 200 kg N ha^{-1} yr^{-1}. A similar maximal plant density (3·2 plants dm^{-2}) and an average plant radius of 0·8 cm was found by van Loo (1991) at the highest seeding rates in a plant density experiment at 480 kg N ha^{-1} yr^{-1} and 3- to 4-weekly defoliation. Therefore it is assumed that with this defoliation regime 3 plants dm^{-2} is the equilibrium plant density in well-established perennial ryegrass swards at a high nitrogen fertilization.

Curve c in Figure 2a shows the result of a

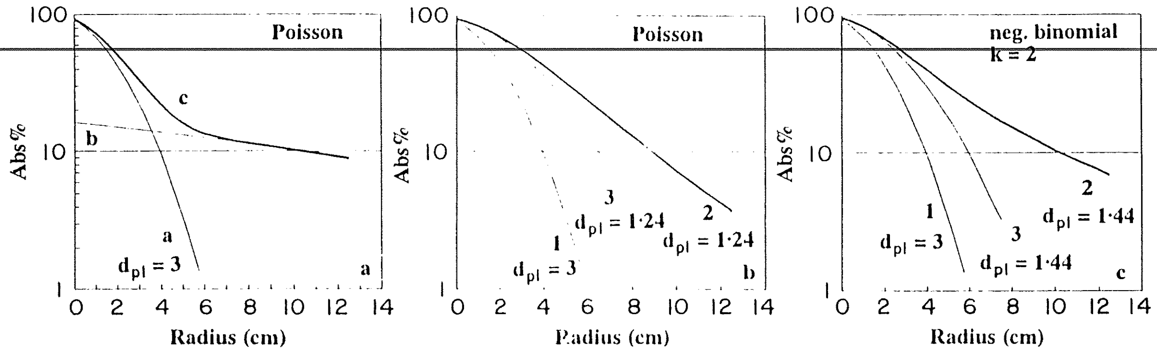

Figure 2. Calculated absence frequencies (Abs%) of plants from quadrats for three theoretical cases of sward damage due to urine excretions over a period of 3 years. (a) 8% of all urine excretions caused bare patches; (b) and (c): each urine excretion caused a local decline in plant density by a factor of 0·4. In (a) and (b) the Poisson function, and in (c) the negative binomial function, was used for calculating the distribution of excretal patches. For the assumptions and details about the different curves see text. d_{pl} = mean number of plants dm^{-2}.

compound absence frequency calculation according to equation (6) for the theoretical case that in a sward with on average 3 plants dm^{-2}, over a period of three years, 8% of all urine excretions would have caused bare patches. This corresponds with 5·7% cover over one grazing season and is near the 7·9% annual sward damage due to urine scorch reported by Lantinga *et al.* (1987) for a sandy soil at an annual fertilizer rate of 400 kg N ha^{-1}. The absence frequency curves for the equilibrium plant density only (curve a) and due to urine patches only (curve b) are also presented. Curve a was calculated according to equation (1) using z_{pl} from equation (3); curve b was calculated from equation (4), using $z_{gap'}$ from equation (5).

Curve 2 in Figures 2b and 2c was calculated under the assumption that starting from an equilibrium density of 3 plants dm^{-2}, each urine excretion would have resulted in a local decline of the plant density by a factor of 0·4. The calculations were also made for a period of three years. In Figure 2b the area proportions of points hit 0, 1, 2, 3 etc. times by urine excretions were calculated according to the Poisson function (equation 8); in Figure 2c these proportions were calculated according to the negative binomial function (equation 9). In both cases, plants were assumed to be Poisson distributed within the respective area proportions. The ultimate absence frequencies were obtained from calculations per area proportion and by summing their values after area correction. The plant diameters in the areas with reduced plant densities were assumed to be gradually larger by a factor (equilibrium density/density)^2.

For the calculations in Figure 2c, a k value of 2 was used in the negative binomial function. This value has been derived from the study of Petersen *et al.* (1956) on the distribution of excreta by grazing cattle. Curve 1 in Figures 2b and 2c was calculated for the case that the whole sward would have had the equilibrium plant density of 3 plants dm^{-2}; curve 3 in the same figures for the case that the whole sward would have had a random plant distribution with the mean plant density of the heterogeneous sward of curve 2.

In all figures the absence frequency is plotted on a log scale against the radius of the sampling quadrats because this illustrates more clearly the change of relationship in the range of large quadrat sizes. All figures illustrate that homogeneous (random) plant distributions lead to convex absence frequency curves (curve a in Figure 2a; curves 1 and 3 in Figures 2b and 2c). For heterogeneous, grazed swards (curve 2 in Figures 2b and 2c) a shift away from convex to a more linear relationship could be expected, while large gaps due to urine scorch might even result in concave curves (curve c in Figure 2a).

Figures 2b and 2c clearly illustrate the specific information which is added by absence frequency estimates to the usual density and cover estimations in characterizing sward structure. In Figure 2b, as well as in Figure 2c, the swards represented by curves 2 and 3 had the same mean plant density and mean cover percentages, but a clearly different spatial structure. To make cover estimations in the field situation which would distinguish both curves from curve 1 in the same figures would have been very laborious

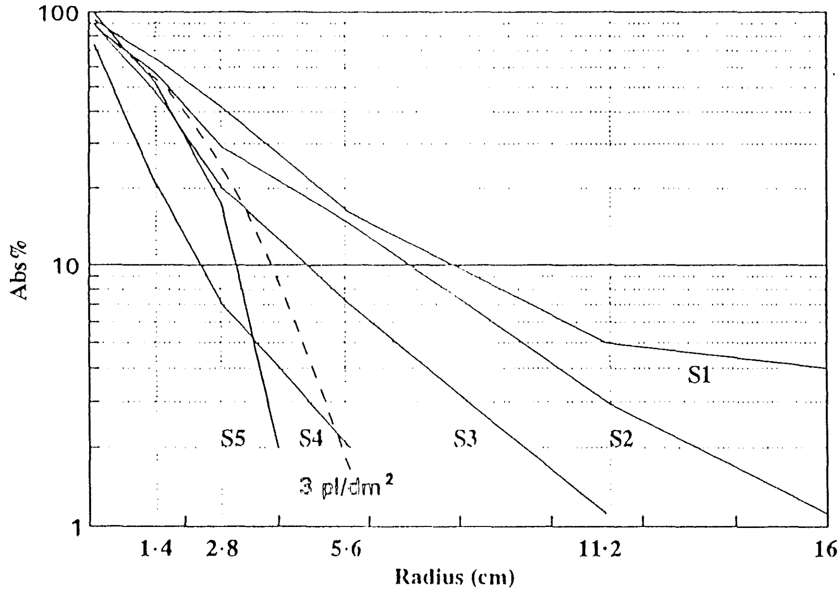

Figure 3. Absence frequency percentages (Abs%) of rooted tiller bases of perennial ryegrass from circular sampling quadrats of different radius sizes. Data from five grassland swards: S1, S2 and S3 (rotational grazing), S4 (continuous grazing) and S5 (3- to 4-weekly mown swards). The dashed line is the theoretical curve for 3 plants dm^{-2} (random plant distribution) and a plant radius of 1 cm.

because the sward represented by curve 1 had only a few percentage points lower cover. In most grassland research, tillers rather than plants are counted because single plants are difficult to distinguish. However, for these the same problem holds, namely that density estimations do not give information on the spatial structure of the sward. Moreover, tiller counting is as laborious as cover estimation.

Curves from field data

Figure 3 presents absence frequency curves of rooted perennial ryegrass tillers as measured in five different perennial ryegrass swards. In these swards, absence frequencies were recorded in concentric rings of the following diameters with the areas shown in brackets: 0·125 cm (point quadrat), 1·4 cm (0·0625 dm^2), 2·8 cm (0·25 dm^2), 5·6 cm (1 dm^2), 11·2 cm (4 dm^2) and 16 cm (8 dm^2). The swards represent three paddocks under rotational grazing on sand (S1, S2 and S3), one paddock under continuous grazing on clay (S4) and plots mown at 3- to 4-weekly intervals on sand (S5). The measurements were made in April 1988 after a mild winter (100 records per paddock). All swards were fertilized with about 400 kg N ha^{-1} yr^{-1}. This is the present Dutch standard fertilizer recommendation for grassland on clay and sandy soils. In Figure 3 the theoretical curve for the equilibrium density of 3 plants dm^{-2} and a plant radius of 1 cm for sown young perennial ryegrass swards, according to Kreuz (1969) and van Loo (1991), is also presented. This is the same as curve 1 in Figures 2b and 2c.

The absence frequency curves are approximately linear to slightly concave with R which suggests that the swards had a heterogeneous plant density and, in the case of sward S1, large bare patches. The figure illustrates the variation in curves that can be expected in intensively used grasslands. Swards S4 and S5 may be classified as good swards, when compared with the theoretical curve. The lower absence frequencies from the two smallest quadrat sizes in curve 4 might be characteristic for continuous grazing. Swards S1 and S2 were very open and had been recommended for reseeding.

Distinct from its statistical significance, which depends on the number of observations, curve S1 indicates that 4% of the paddock consisted of points (areas) with distances to nearest plants of 16 cm or more. The sward further consisted of (5 − 4 =) 1% of areas with nearest plant distances between 11·2 and 16 cm, and of

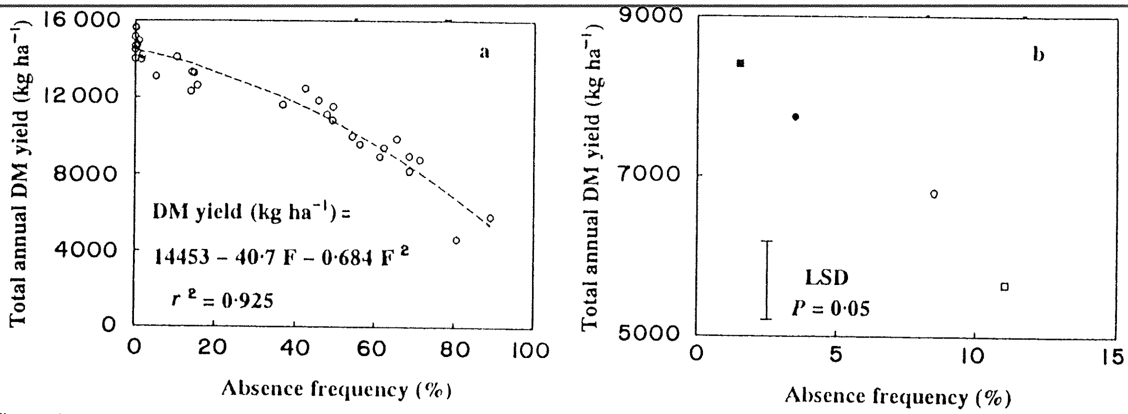

Figure 4. Relation between total annual dry matter yield and absence frequency in a ring with radius of 8 cm, in two experiments with perennial ryegrass. From van Loo (1991). (a) Plant density experiment. Points represent values per plot. (b) Grazed swards. Points represent means per genotype.

(16 – 5 =) 11% of areas with nearest plant distances between 5·6 and 11·2 cm. The remaining 84% of the sward consisted of areas with nearest plant distances of less than 5·6 cm.

Practical implications

Relationships between absence frequencies and yield

The relationship between absence frequencies and grassland yield was studied by van Loo (1991). In his investigations, absence frequency curves were determined in spring in a cutting experiment and in late summer in a grazing experiment and then related to the annual total dry matter yield. The cutting experiment comprised 32 plots with different plant densities of perennial ryegrass cv. Wendy (Anonymous, 1991). The plots had been sown in the preceding autumn at 8 seeding rates in 4 blocks; plant densities in spring varied between 0·1 and 3·3 plants dm^{-2}. The grazing plots were part of a 3-year-old experiment for cultivar evaluation. Four genotypes of perennial ryegrass contrasting in persistency under rotational grazing had been selected (4 plots per genotype).

According to expectation, in the newly sown swards of the cutting experiment, convex Poisson curves were found for absence frequencies plotted on a log scale against quadrat size; in the grazing experiment the curves were approximately linear.

In both experiments correlations between annual dry matter yield and absence frequency were highest in rings with a radius of 8 cm, because with that ring size the absence frequencies showed strongest variation. The relations are shown in Figure 4. The marked difference in the exact relationship between dry matter yield and the absence frequency in the two experiments illustrates the high tillering capacity of perennial ryegrass. In the cutting experiment plants continued to grow in size until the end of the growing season, leading to yield reductions of less than 10% at an absence frequency of 10% measured in spring. At the same value of absence frequency in the grazing experiment, measured in late summer, a yield reduction of about 30% was established, reflecting the openness of the sward throughout the grazing season. The method therefore seems to be promising for inclusion in systems of evaluating cultivars.

Comparison of cultivars

Figure 4b indicated that absence frequency estimates can be used to detect cultivar differences in sward structure. The same is demonstrated in more detail in Figure 5a. Figures 5a and 5b and Figure 6 illustrate different aspects of sward density, and the benefit of combining tiller counts and absence frequency estimations.

The curves in Figure 5a refer to the perennial ryegrass cultivars Madera and Belfort, and were measured in an experiment in which 12 cultivars

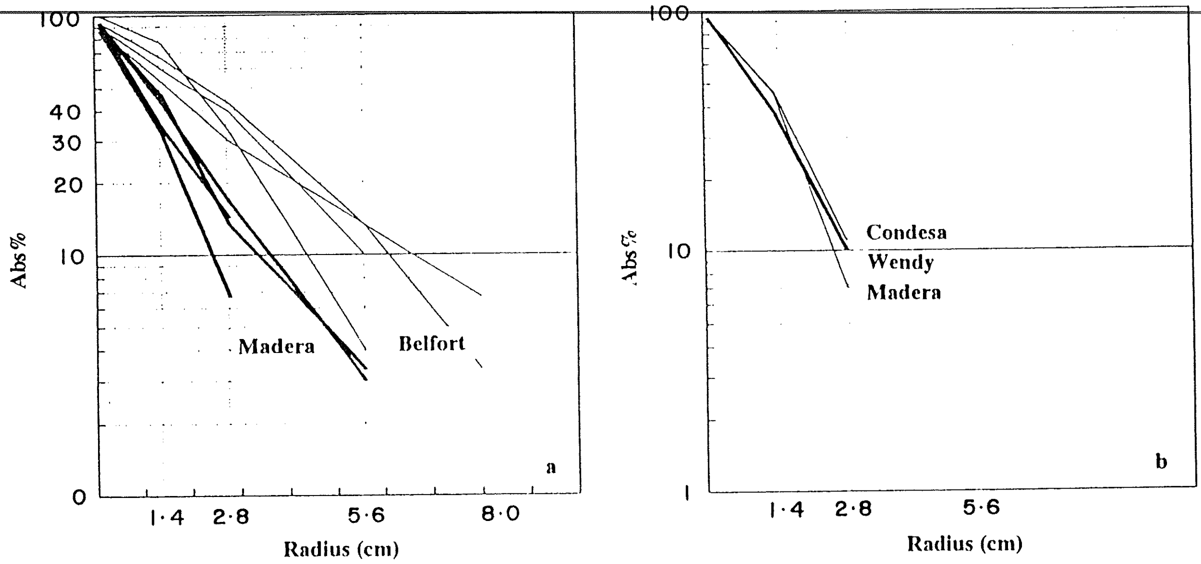

Figure 5. (a) Absence frequency curves of the tetraploid perennial ryegrass cultivars Madera and Belfort in a grazing experiment on sand, August 1988. (b) Absence frequency curves of the perennial ryegrass cultivars Wendy, Condesa and Madera in a grazing experiment on clay, August 1989.

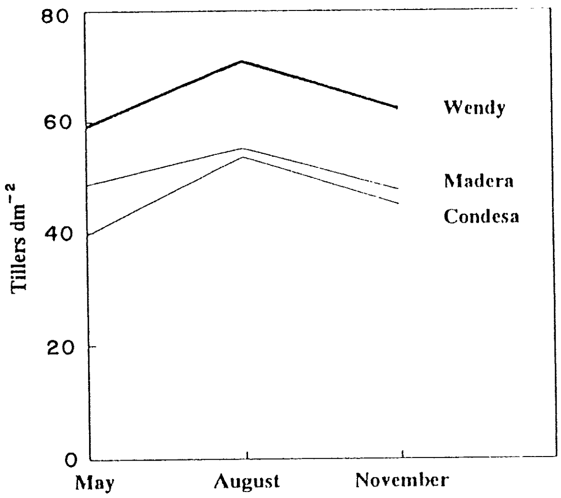

Figure 6. Tiller densities of Wendy, Condesa and Madera at three consecutive sampling dates in 1989, in the grazing experiment on clay.

were compared under rotational grazing in one field. The experiment was carried out on a sand soil; the cultivars were sown in September 1983 in plots of $9 \times 3 \cdot 60$ m, in 4 replicates. The plots were fertilized on the basis of 360 kg N ha^{-1} yr^{-1} and grazed 7 times annually. The curves were estimated in 1988, three weeks after the third grazing. Madera is a new tetraploid perennial ryegrass cultivar on the Dutch recommended variety list (Anonymous, 1991). Both cultivars are bred in The Netherlands. In comparisons in The Netherlands (Anonymous, 1983 and 1987), persistence ratings of 8·0 and 6·5 were assigned to Madera and to Belfort respectively (ratings on a scale from 0 to 10).

Despite the low number of only 30 observations per plot, the Belfort plots scored higher absence frequencies for almost all quadrat sizes, indicating that they had a more open sward structure.

The data from Figure 5b and Figure 6 refer to a comparison under grazing of three perennial ryegrass cultivars: the diploid Wendy and the tetraploids Madera and Condesa (Anonymous, 1991). The grazing experiment was on clay; the cultivars were sown in spring 1988 in plots of 0·75 ha per cultivar, and fertilized on the basis of 400 kg N ha^{-1} annually; the plots were rotationally grazed. In all plots tillers were counted in 0·25 dm^2 cores prior to each grazing (100 cores per plot), while after grazing, absence frequency estimations were executed (100 estimations per plot).

Wendy had a significantly higher tiller density (Figure 6) but a similar absence frequency curve compared with Madera and Condesa (Figure 5b). The lower tiller densities of Madera and Condesa agreed with the visual observation that after each grazing they had a more open sward. However, the similarity of absence frequency curves suggests that this was not due to larger plant interspaces as in the case of Belfort in Figure 5a. The more open sward of Belfort might have been due to plant death as a consequence of a lower persistency; the more open sward of Madera and Condesa might have been due to weak tillering (Neuteboom *et al.*, 1988).

Discussion and conclusions

It is argued that absence frequency recordings in sampling quadrats give very useful information on the spatial structure of grass swards. The absence frequency method resembles the distance method of Keuls *et al.* (1963) for density estimations of plant or animal species. However, it differs from it because with the latter method distances are measured from observation points to the centres of plants, whereas with our method, frequencies of distances are estimated from observation points to the edge of plants.

Equations (1) to (6) can be used to calculate the possible contributions of, for instance, urine scorch patches to the unproductive area of a sward. However, care should be taken to derive definite numbers of open patch sizes from estimated absence frequency curves, because different distribution patterns of open patch sizes can yield the same curve. For detailed analysis of heterogeneity in vegetation types, a variety of quadrat variance methods have been developed (Jupp and Adomeit, 1981; Greig-Smith, 1983). Dale and MacIsaac (1989) have produced a quadrat variance method for detecting patch and gap sizes. However, this method has been developed for detailed studies of succession processes in vegetation. Moreover, quadrat variance methods are very laborious.

Presence or absence frequencies of rooted perennial ryegrass tillers from successive quadrat sizes can be estimated easily by using sets of concentric rings; 100 recordings (inclusive of point quadrats) can be made in a field of 1 ha within 2 h. The absence frequency method is much faster than cover estimations by point quadrat or plant or tiller counts in quadrats and, as was explained in Figures 2b and 2c, gives more complete information on the openness of a sward.

The model calculations in Figure 2 show that the variation in shape of the curves (curvilinear or nearly linear) is theoretically to be expected. This means that for establishing absence frequency curves, a number of concentric quadrat sizes should always be used. The implications of the different shapes of the curves for studying absence frequency–yield relationships in grassland need further investigation.

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