6

Asymmetric insolation interception and consequences for leaf growth in *Deschampsia caespitosa* tussocks

Kristiansen, J.N. & Fox, A.D.

Asymmetric insolation interception and consequences for leaf growth in *Deschampsia caespitosa* tussocks

Jens Nyeland Kristiansen & A.D. Fox

Abstract

In this study we compared leaf density and growth rate of tillers on northern and southern fringes of *Deschampsia caespitosa* tussocks to account for the asymmetric distribution of green biomass around the tussocks in Icelandic hayfields in spring. Southern fringes were characterised by higher leaf density and growth rate of individual tillers. Average light intensity and soil surface temperatures were highest on the southern sides throughout the study period. Most dead litter accumulated on the northern side of the tussock. We suggest that enhanced interception of solar radiation and higher temperatures on southern fringes, together with shading effects of litter on the northern edge contribute to the asymmetry in spring growth of *D. caespitosa* tussocks.

Introduction

Early growth of plants during spring in northern latitudes is triggered by increasing day length as well as rising temperatures. However, differences between plant species in the initiation of growth occur due to different response thresholds to these external factors (e.g. Peacock 1976). Within species differences in phenology also occur. Initiation of growth in individual plants growing on north facing slopes may be delayed compared to those growing on south facing slopes due to differences in interception of solar radiation. Tussock growing plants may create a microclimate in which temperatures between the tussocks may differ from ambient temperatures and hence, benefit those plant species growing between the tussocks (Grosvernier et al. 1995). However, this phenomenon is also likely to affect the tussock forming species themselves. Some tussock growing grasses have been reported to show differences in light interception resulting in differences in productivity between the top surface of the tussock and the sides (fringes) due to the self-shading effect (Caldwell et al. 1983).

In Icelandic hayfields, one of the common and native grass species, *Deschampsia caespitosa* (Thorvaldson 1996) has an open tussock growth form and evidence of differences in biomass and nutrient content between northern and southern fringes in these tussocks has been reported suggesting differences in the microclimate (Kristiansen et al. 1998). Our objective in the present study was to investigate whether northern and southern fringes differed in shoot density and lamina growth rates and if such difference were found, to propose possible abiotic and biotic explanations for the observed asymmetry.

Study site

Fieldwork was conducted at Hvanneyri Agricultural College in Borgafjördur, south west Iceland (64°34'N 21°46'W) during 19 April to 7 May 1998. The college comprises some 90 hayfields of which *Poa pratense*, *Phleum pratense*, *Alopecurus* sp. and *D. caespitosa* are the predominant species in the sward. The study was carried out in a *D. caespitosa* dominated hayfield not subject to grazing by herbivores.

Methods

Biomass and growth measurements

From each of 25 randomly chosen tussocks (c. 40 cm diameter) the number of lamina (leaves) were counted in a 3 x 3 cm square on the northern and southern quadrants of the tussocks (i.e. within 45° of either side of these cardinal points). Ten tillers (shoots) on north and south fringes of one randomly chosen tussock were individually marked with paper tags attached with cotton loops. The length of all lamina on each tiller was measured (that is including those present at the start of the study and all lamina which developed subsequently) on 19 April and again on 7 May.

Environmental measurements

Light intensity (lux) was measured using a lux meter, placing the sensor horizontally directly at the foot of the northern and southern sides of six *D. caespitosa* tussocks and recorded every hour from 06.00 – 19.00 on 20 April, 2 May and on 6 May. Miniature thermistor probes attached to temperature dataloggers were placed in a similar manner north and south of one randomly chosen typical tussock measuring soil surface temperature every half hour from (20 April – 6 May). The dead litter (grass leaves) from the previous growth season seemed to have been accumulated in a consistent direction and therefore to test this hypothesis the compass direction with most abundant litter collection was determined for 50 tussocks.

In comparing biomass (number of green leaves) on northern and southern fringes of tussocks pair-wise t-tests was used and comparing growth rates ordinary t-test was used. Repeated measures analysis of variance (ANOVA) (SAS Institute Inc. 1990) was used to test for difference in light interception between northern and southern fringes of tussocks during 06:00-19:00 on 20 April, 2 May and 6 May.

Results

Biomass and rate of leaf extention

There were significantly more leaves on the southern sides of the tussocks compared to the north (south: mean = 15.44 leaves $\pm$ 1.12 SE 3 x 3 cm^{-2}, n = 25; north: mean = 11.04 leaves $\pm$ 0.98 SE 3 x 3 cm^{-2}, n = 25; paired t-test: $t = 4.4$, $DF = 24$, $p < 0.001$). In addition, tillers on the southern fringes provided higher growth rate in terms of cumulative leave elongation (south: mean = 22.1 mm $\pm$ 1.3 SE, n = 10; north: mean = 14.4 mm $\pm$ 2.68 SE, n = 10; t-test: $t = 2.584$, $DF = 13$, $p < 0.05$). There was a tendency towards higher production of lamina (numbers per yiller) on the southern fringes (south: mean = 0.8 lamina ± 0.13 SE, n = 10; north mean = 0.5 lamina ± 0.17 SE, n = 10; t-test: t = 1.406, DF = 18, p = 0.18) and that the growth (elongation) of these were higher than those on the northern sides (south: mean = 12.7 mm ± 2.53 SE, n = 10; north: mean = 6.8 mm ± 2.35 SE, n = 10; t-test: t = 1.708, DF = 18, p = 0.10) although this was not quite significant at the $\alpha = 0.05$ significance level.

Solar radiation

Mean light intensities from 20 April, 2 May and 6 May are shown in Fig. 1. Repeated measures ANOVA showed significant differences between north and south of the tussocks on all dates (20 April: $F_{1,11} = 30.25$, $p < 0.01$; 2 May: $F_{1,11} = 33.88$, $p < 0.01$; 6 May: $F_{1,11} = 25.20$, $p < 0.01$) south always receiving more solar radiation. There was no tussock effect on the first two dates (20 April: $F_{5,11} = 1.08$, ns; 2 May: $F_{5,11} = 4.51$, ns) but on 6 May there was a significant difference between tussocks ($F_{5,11} = 9.77$, $p < 0.05$).

Temperature

Daily minimum and maximum temperatures are shown in Fig. 2. Minimum temperatures were almost identical on the southern and northern sides of the tussock as these occurred at night. Maximum temperatures however, were almost always markedly higher on the southern compared to the northern side.

Leaf litter

Most old dead leaves (i.e. from the previous year) were bending in a northerly direction (382.1 °N, ± 5.88 SE, n = 45) probably caused by the predominating winds during the preceding autumn/winter.

Discussion

Southern fringes of the *D. caespitosa* tussocks supported the highest density of leaves and hence the highest amount of green material in agreement with previous findings reported for this grass species in Iceland (Kristiansen et al. 1998). Furthermore, the present study also revealed a higher lamina growth rate amongst individual tillers on the southern fringes compared to those growing on the northern sides. In our earlier study of *D. caespitosa*, tillers on the southern fringes were shown to have highest protein content (Kristiansen et al. 1998). High protein content of plant tissue is associated with sites of intense enzyme activity such as those plant parts showing the most intense growth (Robson & Parsons 1978).

Dry matter production in grass species is, among other things, related to the quantity of light energy available (Holmes 1980). The efficiency with which light is converted by grass will depend on the photosynthetic activity of individual leaves, their arrangement within the sward and the proportion of the light energy falling on a given area that is intercepted by green leaves (Holmes 1980). The importance of foliage orientation to the productivity of plants has been demonstrated by e.g. Caldwell et al. (1983) and Ryel et al. (1993) who found a difference between the top surface and the side of tussocks. In our study the difference in growth pattern might have been due to such a self shading effect, northern fringes receiving significantly less light energy. Tillers growing in tussocks have been shown to have lower photosynthetic efficiency than tillers distributed uniformly due to shelf shading within the tussock (Ryel et al. 1994). Furthermore, the observed accumulation of dead litter on the northern fringe of tussocks (i.e. the previous years production of leaves, pers. obs.) may also have also added to the shading effect in *D. caespitosa* in this study. Growth of grasses is both affected by temperature and solar radiation (Russel 1973, Holmes 1980, Lewis 1986), two environmental factors which are closely correlated. We found a clear difference between maximum temperatures on the northern fringes compared to the southern; the southern sides always being subject to the highest temperatures. Temperature difference on such a small scale in tussocks is a phenomenon known to result from the differential interception of solar radiation (Hansen 1973). Early in the growing season, the low angle of incident solar radiation probably resulted in greater light intensities on the southern fringes of the tussocks thus, creating both higher temperatures and better conditions for photosynthesis than on the northern faces. In this study maximum temperatures rarely exceeded 10 °C on the northern side of the tussock in contrast to the southern side where maximum temperatures reached as high as 15-20 °C. High temperatures will enhance mineralisation in the soil and hence, increase the availability of nitrogen and phosphorous to the plants (Russel 1973, Lewis 1986, Schmidt et al. 1999). Grasses exhibit an opportunistic growth strategy and are therefore very sensitive towards nutrient mobilisation and immobilisation (Michelsen et al. 1999). Furthermore, the growth rate of the youngest visible leaf of grasses has been shown to be very sensitive to temperature (Williams & Biddiscompe

1965), but insensitive to short term changes in radiation (Allison 1963). Moreover, solar radiation is not the only determinant of temperature in the context of the microclimate of the tussocks, since even light winds can cause considerable loss of heat because they remove the layer of warm air close to the ground (Corbet 1972). This environmental factor was unfortunately not measured in the present study.

One of the consequences of the asymmetric growth of *D. caespitosa* tussocks is that herbivorous geese mainly exploit the higher quality food on the southern fringes to optimise their nutrient intake (Kristiansen et al. 1998) and possible other herbivorous animals utilise this in a similar manner. Grazing animals can affect the growth pattern and nutrient content of their forage plant species or parts (e.g. Fox et al. 1998), therefore, it is interesting to speculate and investigate how and if such foraging affects the growth pattern and hence, the shape of *D. caespitosa* tussocks.

Such asymmetric growth of tussock growing graminoids due to different light interception, temperature and/or the self shading effect by accumulation of dead litter has to our knowledge, not been recorded before. Unfortunately we were unable in this study to demonstrate the effect of each of these factors separately. Hence, to finally establish a more fine grained causality it is necessarily to carry out experimental studies to be able to control each environmental factor.

Acknowledgements

We are grateful to the staff of the Hvanneyri Agricultural College, especially Björn Thorsteinsson for permission to work at the farm fields. We thank Anders Michelsen and Staffan Karlsson for useful comments on the manuscript.

References

Allison, R. M. 1963. Phasic growth of the leaves of cereales. - Nature, Lond. 198: 809-10.

Caldwell, M. M., Dean, T. J., Nowak, R. S., Dzurec, R. S. & Richards, J. H. 1983. Bunchgrass architecture, light interception, and water-use efficiency: assessment by fiber optic point quadrats and gas exchange. - Oecologia 59: 178-184.

Corbet, P. S. 1972. The microclimate of arctic plants and animals, on land and in fresh water. - Acta Arctica 18: 1-43.

Fox, A. D., Kristiansen, J. N., Stroud, D. A. & Boyd, H. 1998. The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. - Oecologia 116: 154-159.

Grosvernier, P. H., Matthey, Y. & Buttler, A. 1995. Microclimate and physical properties of peat: New clues to the understanding of bog restoration processes. - In: Wheeler, B. D., Shaw, S. C., Fojt, W. J. and Robertson, R. (eds) Restoration of temperate wetlands: John Wiley & Sons, New York.

Hansen, K. 1973. Microthermic observations in arctic vegetation. - Meddelser om Grønland, Bioscence 194(6).

Holmes, W. (ed.) 1980. Grass, its production and utilization. - British Grassland Society, London.

Kristiansen, J. N. Fox, A. D., Stroud, D. & Boyd, H. 1998. Dietary and microtopographical selectivity of Greenland white-fronted geese feeding on Icelandic hayfields. - Ecography 21: 480-483.

Lewis, O. A. M. 1986. Plants and nitrogen. Studies in biology no. 166. - Edward Arnold, London.

Michelsen, A., Graglia, E., Schmidt, I. K., Jonasson, S., Quarmby, C. & Sleep, D. 1999. Differential responses of grass and dwarf shrubs to long term changes in soil microbial biomass, C, N and P, following factorial addition of NPK fertilizer, fungicide and labile carbon to heath. - New Phytologist 143.

Peacock, J. M. 1976. Temperature and leaf growth in four grass species. - J. Appl. Ecol. 13 (1): 225-232.

Robson, M. J. & Parsons, A. J. 1978. Nitrogen deficiency in small closed communities of S24 ryegrass, 1. Photosynthesis, respiration, dry matter production and partition. - Ann. Bot. 42: 1185-1197.

Russell, E.W. 1973. Soil conditions and plant growth. - Longman, London.

Ryel, R. J., Beyschlag, W. & Caldwell, M. M. 1993. Foliage orientation and carbon gain in two tussock grasses as assessed with a new whole-plant gas-exchange model. - Funct. Ecol. 7: 115-124.

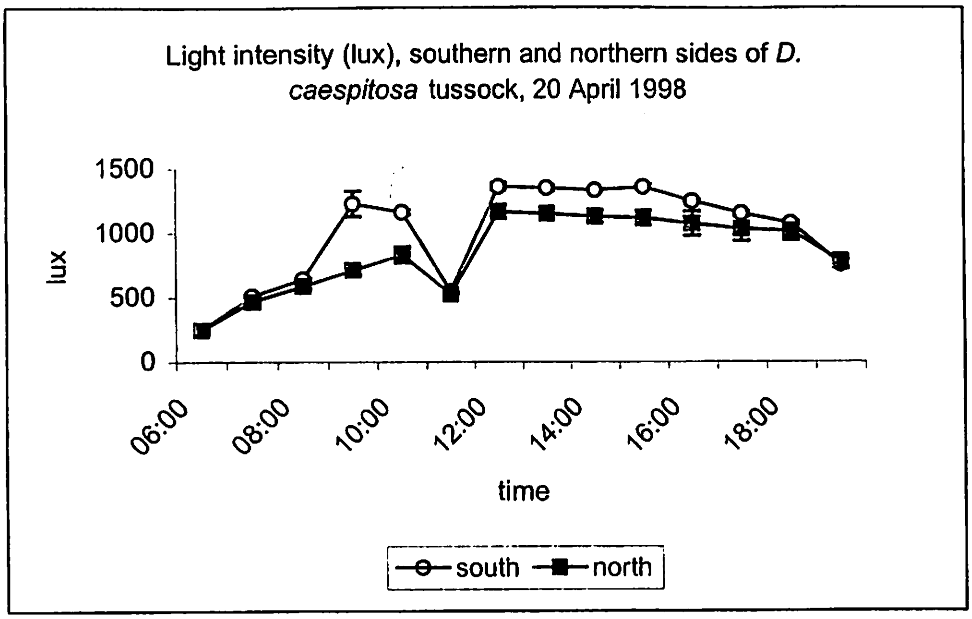
Ryel, R. J., Beyschlag, W. & Caldwell, M.M. 1994. Light field heterogenity among tussock grasses: Theoretical considerations of light harvesting and seedling establishment in tussocks and uniform tiller distributions. - Oecologia 98: 241-246.

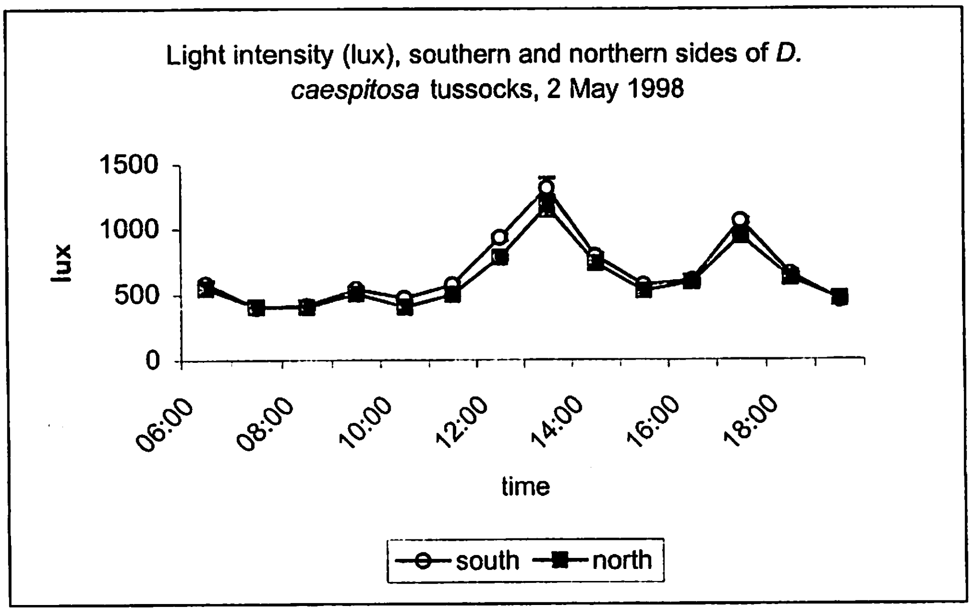
SAS 1990. SAS user's guide: SAS/STAT, version 6. - SAS Institute Inc.

Schmidt, I. K, Jonasson, S. & Michelsen, A. 1999. Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. - Applied Soil Ecology 11: 147-160.

Thorvaldson, G. 1996. Botanical composition of Icelandic grass fields. - Acta Agriculturae Scandinavica Section B Soil and Plant Science 46(2): 121-127.

Williams, C. N. & Biddiscombe, E. F. 1965. Extention growth of grass tillers in the field. - Aust. J. agric. Res. 16: 14-22.





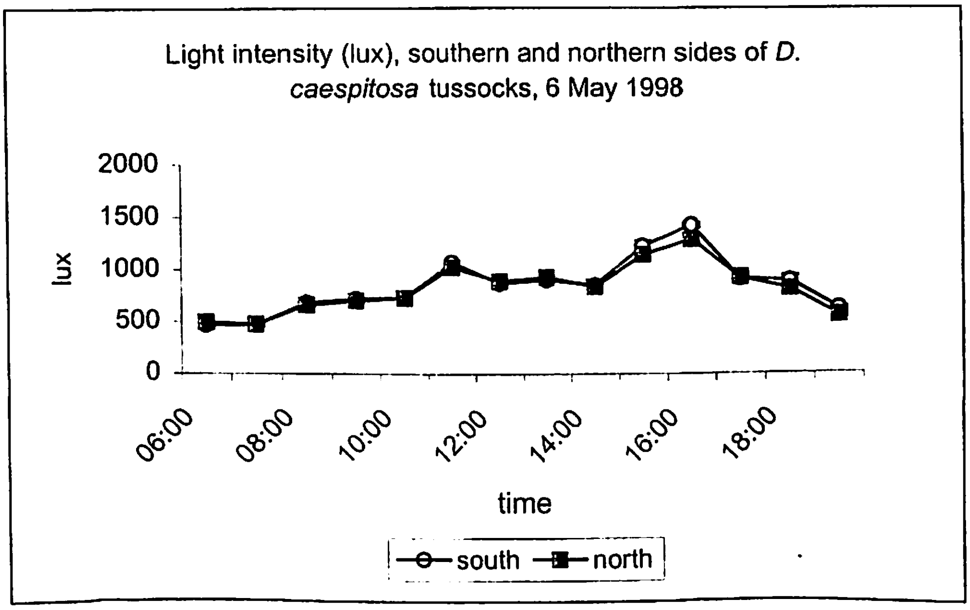


Fig. 1. Solar interception (lux) on southern and northern fringes of *D. caespitosa* tussocks during 06:00 to 19:00 on 20 April, 2 May and 6 May, 1998. Mean $\pm$ SE, n = 6 tussocks.

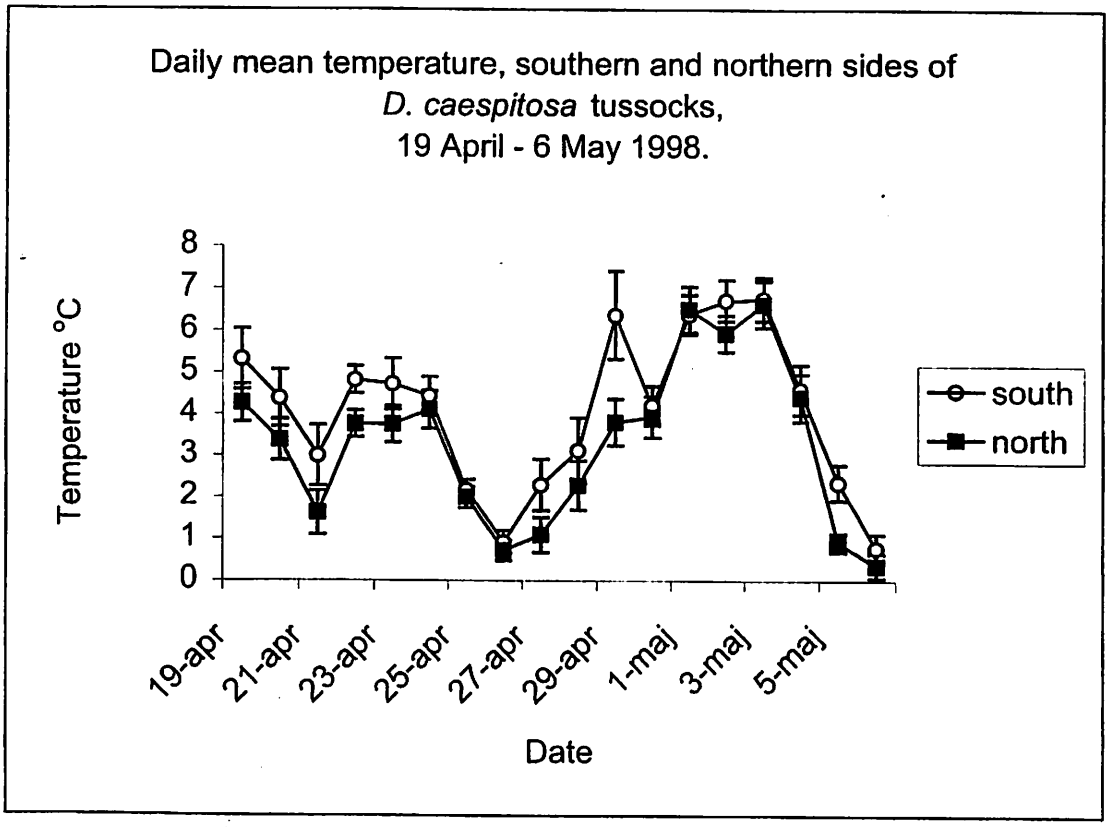


Fig. 2. Minimum and maximum temperatures (°C) on the southern and northern fringe of a *D. caespitosa* tussock, 20 April – 7 May, 1998.