

The influence of goose grazing on the growth of *Poa arctica*: overestimation of overcompensation

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The effect of grazing by barnacle geese (*Branta leucopsis*) on above-ground production was investigated on the Arctic tundra grass *Poa arctica* at Spitsbergen during the growing season of 1996. We applied three treatments: grazed, whole season ungrazed and temporary ungrazed during the second half of the season. In each treatment individual shoots were marked and their leaves regularly measured to calculate production. Production was calculated in three different ways: Increment in Standing Crop (ISC), Above-ground Biomass Production (ABP) and leafbirths. ISC in temporary and permanent exclosures is the most commonly used method, but it neglects senescence and disappearance of biomass during the experiment. In our study, ISC of grazed *Poa arctica* was significantly higher than of ungrazed swards. However, the flow of senescing biomass was much larger in ungrazed swards compared to grazed swards. Thereby an overestimation of overcompensation was introduced. Calculation of ABP takes this flow of senescing biomass into account. In terms of ABP, *Poa arctica* did not overcompensate the losses due to goose grazing. Accordingly, the number of leafbirths did not differ between grazed and ungrazed swards. In several other studies, where senescence and disappearance of leaves were neglected, inclusion of these fluxes would at least decrease overcompensation. Therefore, we advocate regarding senescence and disappearance of leaves while measuring overcompensation.

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The response of plant production to grazing is subject of many studies. An important question in these studies is, whether grazing stimulates above-ground plant growth. Such a stimulation is often referred to as overcompensation (Belsky 1986), which means that the production of grazed plants exceeds the production of ungrazed plants. This phenomenon has led to herbivore optimization models, which predict that the level of overcompensation is dependent on the intensity of grazing (McNaughton 1979, Hik and Jefferies 1990).

Overcompensation has been found in several studies (Milchunas and Lauenroth 1993). In Arctic systems, overcompensation by goose grazing has been found by Cargill and Jefferies (1984), Kotanen and Jefferies (1987) and Bazely and Jefferies (1989). This positive effect is explained by an increased availability of nutrients from goose faeces (Bazely and Jefferies 1985).

However, in other Arctic studies overcompensation was not found (Kotanen and Jefferies 1989, Zellmer et al. 1993, Gauthier et al. 1995). Therefore, the generality of the occurrence of overcompensation is still not clear.

Quantifying production is principally difficult when there is a potential for overcompensation and part of the production is consumed by herbivores (McNaughton et al. 1996). In this paper, we stress an additional problem of senescence and disappearance of biomass from exclosed plots during the experiment. This is, often implicitly, considered a minor problem when grazed swards are measured over short intervals.

We investigate the occurrence of overcompensation in the Arctic perennial grass *Poa arctica* L., when grazed by wild barnacle geese (*Branta leucopsis* Bechstein) and evaluate the importance of measuring senescence of leaves in a comparison of grazed and ungrazed swards.

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Table 1. Example of calculations with data collected by measuring leaf elongation on individually marked shoots. All values are in mm shoot⁻¹. l = living, g = grazed and d = dead leaf. When a leaf is grazed, production cannot be calculated and a missing value (MV) is given.

| Date | Leaf 1 | Leaf 2 | Leaf 3 | St. Crop | Production | Leaf-births |
|---------|--------|--------|--------|----------|------------|-------------|
| 5 July | 12 l | 6 l | | 18 | | 0 |
| 11 July | 14 l | 4 g | 2 l | 20 | MV | 1 |
| 18 July | 14 l | 8 g | 13 l | 35 | 15 | 0 |
| 23 July | 14 d | 10 g | 19 l | 29 | 8 | 0 |

Methods

Study area

This study has been carried out in 1996 on the tundra around the village of Ny Ålesund (78°55'N, 11°30'E), Spitsbergen. About 700 barnacle geese moulted their wing feathers and raised their young in this area. Since 1990 the development of the population has been studied intensively. The described study on the impact of geese on production of the vegetation was part of this long-term project.

The tundra at our study site had dry and wet parts. A very common grass species at the wet sites was *Poa arctica*. This was the major food species for barnacle geese. Reindeer (*Rangifer tarandus platyrhynchus*), the only mammalian herbivores, predominantly grazed on the dryer parts. Grazing by barnacle geese started at low intensity in the end of June, when non-breeding birds started moulting. Breeding geese spend June on islands in the fjord, where they nested. From the beginning of July, when the first goslings hatched, the grazing pressure in the study area around the village increased because parents left the islands and moved with their young to the study site. This was the time that our experiment started. At the end of August, when most goslings could fly, the geese left the study area to forage under birdcliffs. At that time the experiment ended. In 1996, the temperature was above 0°C between 4 June and 15 September. Our experimental period covered approximately 75% of total annual plant production (Loonen unpubl.).

Experiments

The investigated plant species was *Poa arctica*, an important food plant for barnacle geese in our study area. Data were collected from 3 July till 20 August in 1996. At seven sites, three sample points were established for three treatments: grazed, ungrazed and temporary exclosed. For the ungrazed treatment, exclosures were built on 3 July 1996 to prevent grazing. On average one metre from the exclosures, grazed sample points were chosen. On 28 July an extra set of exclosures was established (temporary exclosures). The exclosures were made of chicken wire, and had a diameter of approximately 0.5 m. No nutrients were added.

In each sample point, 16 individual shoots were marked with a plastic ring, which was pushed into the moss carpet around the shoots. For determining primary production and standing crop, the lengths of all leaves of marked plants were measured every 7 d throughout the season. Because leaves were always measured starting from the oldest leaf, individual leaves could be recognized and the fate of single leaves could be followed. The data obtained with this method are in millimetres per shoot. By using this method, also leaf-births per shoot and increment in standing crop can be calculated (Table 1).

Once every 15 d a sample of 300–500 leaves was measured, dried and weighed to transform production data from millimetres into grams. This enables comparison with other studies although only leaves (i.e. grazable parts) are included in our calculation of production. However, for the purpose of comparing plant production in different treatments, the directly measured values in millimetres will be used.

Data analysis

The 16 shoots at each sample point are pseudoreplicates, therefore only average values per sample point were used. When shoots were grazed, the production in that particular interval could not be measured directly, because it is not possible to distinguish between the amount produced and the amount grazed. In the course of the experiment, almost all shoots were grazed one or more times, but all 16 shoots never were grazed in the same interval. Therefore, production in the grazed sample points was calculated from the shoots which were not grazed in that particular interval. So the average production of a grazed sample point in every interval is calculated from a subset of the 16 plants in that sample point. Because geese might feed selectively on the most productive shoots, measuring only ungrazed shoots in the grazed sample points could cause an underestimation of the production in grazed sample points. The average production of a sample point can be corrected in the following way:

$$\text{Prod.}_{\text{corrected}} = \text{Prod.}_{\text{obtained}} + \text{Fraction grazed} \times \text{Selectivity} \quad (1)$$

Table 2. Characteristics of grazed patches of *Poa arctica*. All values refer to leaf production and leaf standing crop, so stems are not included. In parentheses, the standard error of the mean is given. ABP = Above-ground Biomass Production.

| Variable | Value in mm shoot ⁻¹ | Value in g m ⁻² |
|----------------------------|---|---|
| Density of shoots | 2.0×10^3 (0.13×10^3) shoots m ⁻² | |
| Weight/length ratio | 4.3×10^5 (0.60×10^{-5}) g mm ⁻¹ | |
| Standing crop grazed sward | 20 (1.1) mm shoot ⁻¹ | 1.7 g m ⁻² |
| ABP | 1.2 (0.13) mm shoot ⁻¹ d ⁻¹ | 0.10 g m ⁻² d ⁻¹ |
| Senescence | 0.21 (0.061) mm shoot ⁻¹ d ⁻¹ | 1.85×10^{-2} g m ⁻² d ⁻¹ |

$$\text{Selectivity} = \text{PPI}_{\text{grazed}} - \text{PPI}_{\text{ungrazed}} \quad (2)$$

where PPI = Production Previous Interval.

In words: The correction of the production is proportional to the fraction of the 16 shoots that was grazed in each sample point; the more shoots are grazed, the larger the underestimation of production is. This fraction was multiplied by the selectivity of the grazing geese, which was calculated from the difference in production between grazed and ungrazed plants in the grazed sward. This had to be measured in the interval previous to grazing because it was not possible to calculate the production of a shoot in the interval in which it was grazed. Therefore, the assumption was made that the difference in production between grazed and ungrazed plants in the interval previous to the actual interval was a good estimate for the difference in production between grazed and ungrazed shoots in the actual interval.

For assessing the effect of senescence on the calculation of production, the data are presented in three different ways. Above-ground Biomass Production (ABP) is the sum of all newly produced biomass. In this study, ABP is based on measurements of leaf demography and elongation on individually marked shoots. All production is measured before senescence takes place. Alternatively, senescing biomass can be quantified separately and added to the Increment in Standing Crop (ISC), which is the most commonly used measure (e.g. Cargill and Jefferies 1984). In ISC, standing crop at the beginning of an interval is subtracted from standing crop at the end of an interval. Usually, standing crop is measured by clipping turfs and ISC in temporary enclosures is considered to represent production in grazed swards. In most studies ISC is referred to as Net Above-ground Primary Production (NAPP). We avoid the term NAPP to minimize confusion in our definitions of ABP and ISC. When measuring leafbirths (e.g. Kotanen and Jefferies 1987), production is expressed as the number of newborn leaves per time unit. Production of grazed shoots can be determined without placing enclosures. When production is measured in leafbirths, the assumption is made that leaf elongation is equal in grazed and ungrazed swards. The difference between ISC and both leafbirths and ABP is that leafbirths and ABP are independent of senescing leaves, while ISC assumes that senescence is negligible (see Discussion).

Tests were carried out on the cumulative results of the experiment. When differences fitted the normal distribution (Kolmogorov-Smirnov goodness-of-fit test), the paired sample *t*-test was used for comparisons. In other cases the Wilcoxon matched pairs signed-rank test was applied. The program used for testing was SPSS-PC + . All error bars used in figures demonstrate standard error of the mean.

Results

Table 2 summarizes some characteristics of *Poa arctica* patches in the study area. These patches occur scattered in the moss carpet.

Geese fed selectively on the most productive shoots (t-test: $t = 2.95$; $df = 23$; $P = 0.007$, Fig. 1). This selectivity made correction of grazed production with formula (1) necessary to avoid underestimation of production in the grazed treatment. There is no time trend in selectivity (ANOVA: $F = 1.29$; $df = 1,6$; $P = 0.313$), so the average selectivity (0.37 mm shoot⁻¹ d⁻¹) could be used for all intervals.

The standing crop of the grazed treatment remained more or less constant, whereas the standing crop in the enclosure initially showed an increase, which flattened towards the end of the season (Fig. 2). The Above-ground Biomass Production was 47.7 mm shoot⁻¹ for

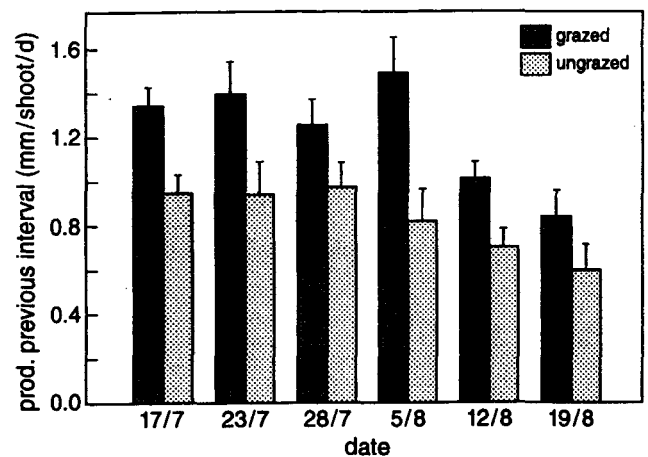


Fig. 1. The difference in production between shoots that are grazed and shoots that are not grazed in a grazed sward, measured in the interval previous to the grazing event. This difference is a result of selective grazing on the most productive shoots.

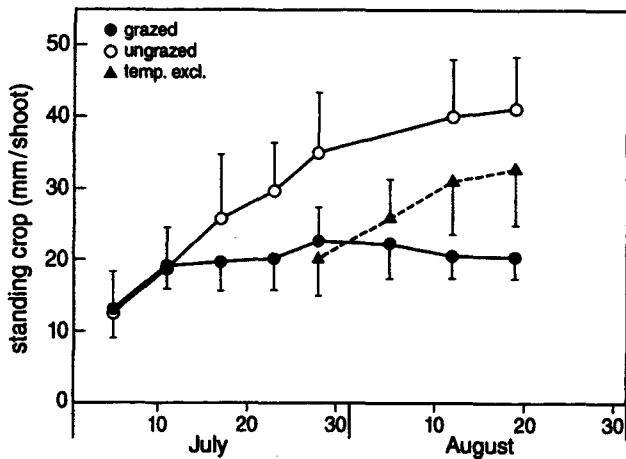


Fig. 2. Standing crop in the grazed, ungrazed and temporary exclosure treatments.

grazed sample points and 46.9 mm shoot⁻¹ for ungrazed sample points. There is no difference in ABP between the grazed and ungrazed treatment (*t*-test: *t* = 0.47; *df* = 6; *P* = 0.656). Increment in Standing Crop (ISC) was significantly different between treatments (*t* = 3.90, *df* = 6, *P* = 0.008). ISC amounted 38.6 mm shoot⁻¹ in the grazed sward and 31.9 mm shoot⁻¹ in the ungrazed sward, which would erroneously suggest overcompensation of 121% in grazed swards. In Fig. 3, both ABP and ISC are calculated from ungrazed swards and temporary exclosed swards. The temporary exclosures represent the grazed treatment, as is usual when the effect of grazing on production is measured as ISC. In the second half of the season the difference between ISC and ABP production becomes clearly visible: The full time exclosure had already a more or less constant standing crop, resulting in a low ISC, where the standing crop in the temporary exclosure was still increasing, which causes a high ISC.

In Fig. 4 production in leafbirths per shoot is plotted using the same set of data as in Fig. 3. The difference in leafbirths between grazed and ungrazed swards is not

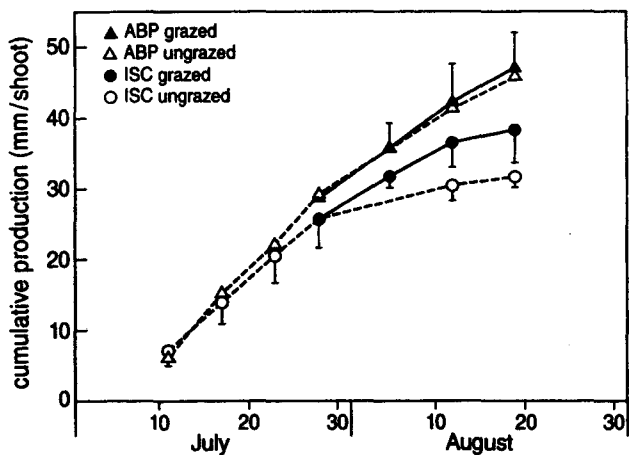


Fig. 3. Above-ground Biomass Production (ABP) and the Increment in Standing Crop (ISC) in grazed and ungrazed swards. The distance between the ABP-line and the ISC-line represents the amount of leaf senescence.

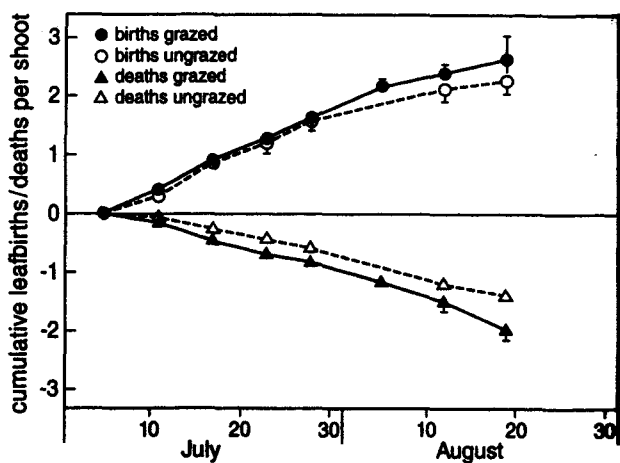


Fig. 4. Leaf turnover in grazed and ungrazed swards, expressed as leafbirths and leafdeaths. For some data points, error bars are not visible because they are smaller than the size of the marker.

significant (*t*-test: *t* = 1.55; *df* = 6; *P* = 0.173). Again, there is no indication for overcompensation. The number of leafdeaths is significantly higher in the grazed sward (Wilcoxon: *Z* = 2.197; *P* = 0.028).

Discussion

The most important difference between ISC and ABP is that ISC gives a value for production excluding senescence of leaves, and both leafbirths and ABP give a value including senescing leaves. The difference between ABP and ISC equals the flux of senescence.

$$\text{ISC} = \text{ABP} - \text{senescence} \quad (3)$$

For the Spitsbergen situation this flux is equal to the distance between the ABP and ISC lines in Fig. 3.

This flux of senescence has two consequences: first, the absolute values of grazed and ungrazed production are much higher when ABP is measured than when ISC is measured. Several authors have stressed this difference (e.g. Davies 1981). Using ISC, sometimes improbable consumption rates of more than 100% of primary production are found, which also indicate an underestimation of production. Second, senescence has important consequences when production of grazed and ungrazed plants is compared. The magnitude of the senescence flux is dependent on the rate of leafdeaths and on the weight of dying leaves. Fig. 4 shows that the rate of leafdeaths is higher in grazed plants. However, the length of these dying grazed leaves is much smaller than the length of dying ungrazed leaves, just because a part of the leaf is already removed by the herbivore. What is grazed cannot die anymore, so a smaller flux of senescence occurs in grazed plants. In other words: a high rate of leaf deaths does not automatically lead to a large amount of dead biomass in grazed plants. From

ABP of ungrazed plants, a large flux of senescing leaves is subtracted, resulting in a low ISC (Fig. 5). This appears from a steady or even decreasing standing crop, whilst new leaves are still produced at a considerable rate.

ABP and leafbirths reveal no overcompensation though the rate of leafdeaths was higher in grazed swards than in ungrazed swards. A disadvantage of only using leafbirths and deaths is that grazed plants might invest more in extra tillers than in leaf elongation (Lemaire and Chapman 1996), or become morphologically dwarfed. Because these phenomena are not included in the measure of leafbirths and deaths, production of grazed plants could be overestimated compared to ungrazed plants.

Belsky (1986) defined overcompensation, exact compensation and undercompensation as the categories to use for the response of plants to grazing. This has proven to be a useful way to discuss the production of grazed plants. However, these definitions are in terms of increment of standing crop. In this study, it is shown which problems can occur when senescence is neglected in comparing grazed and ungrazed production. Therefore, we propose to incorporate the flux of senescing leaves in the definition of overcompensation.

Most papers which describe experiments measuring standing crop use the term net production or Net Above-ground Primary Production (NAPP), to mean what is called Increment in Standing Crop (ISC) in this paper. Later on, the same results are referred to as

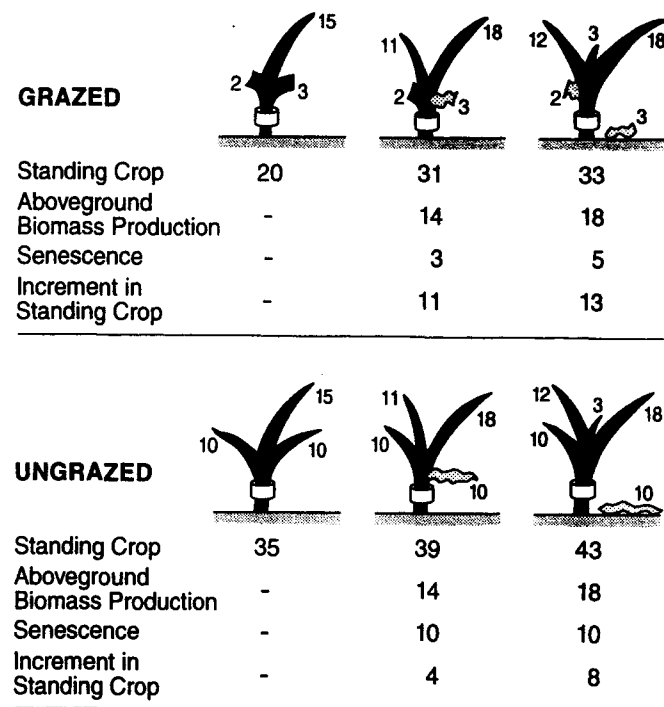


Fig. 5. The development of a grazed shoot and an ungrazed shoot, indicating how differences in standing crop lead to differences in the rate of leaf senescence, thereby affecting the ISC.

Table 3. The ratio of the production of grazed and ungrazed plants. ¹ = Spitsbergen, ² = La Pérouse Bay.

| | Increment in Standing Crop | Above-ground Biomass Production |
|---------------------------------|----------------------------|---------------------------------|
| <i>Poa</i> ¹ | 1.2 | 1.0 |
| <i>Carex</i> ² | 1.8 | 1.3 |
| <i>Puccinellia</i> ² | 1.7 | 1.2 |

'production' and 'growth', which is Above-ground Biomass Production (ABP) in this paper. In this way, it is implicitly assumed that ISC and ABP are the same, thus that the flux of leafdeaths is zero. In this context, ABP is the best synonym for NAPP, where ISC is, just as it says, a measure for changes in the standing crop.

Senescence of biomass is relevant for measuring production or overcompensation. Cargill and Jefferies (1984) found a substantial overcompensation in their study. Because ISC was used to calculate production, overcompensation might have been overestimated. This was already indicated by a stabilization of the standing crop in the course of the growing season, whilst leaf production is still going on (Cargill and Jefferies 1984, Kotanen and Jefferies 1987). Because data on both leafbirths and deaths are published of the same species in the same area, a rough recalculation from ISC, which is given in Cargill and Jefferies (1984) to ABP was possible (Appendix). The conclusion remains that goose grazing caused overcompensation in their study area, although the result for both *Puccinellia phryganeodes* and *Carex subspathacea* is a decrease in the amount of overcompensation (Table 3).

From the island of Schiermonnikoog in the Dutch Waddensea, a count of leafbirths and leafdeaths in the growing season of *Festuca rubra* is available (Fig. 6; Pruis 1990). The number of leafdeaths is almost equal

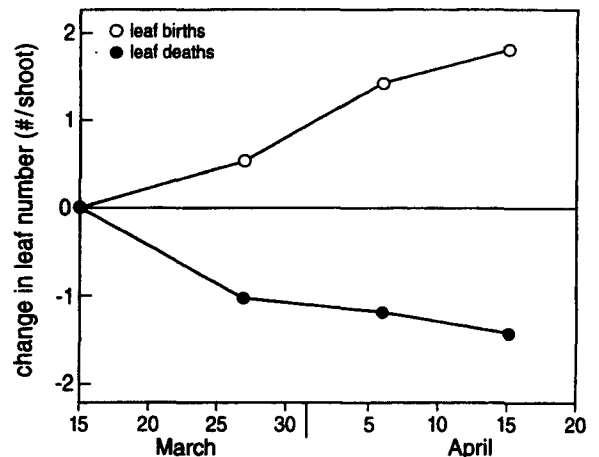


Fig. 6. Leafbirths and leafdeaths of *Festuca rubra* on the temperate saltmarsh of Schiermonnikoog, The Netherlands. Redrawn from Pruis (1990).

to the number of leafbirths, indicating that also in temperate zones senescence may cause an underestimation of production. Wegener and Odasz (1997) showed that senescence of biomass over a winter period differed between grazed and ungrazed plants, thereby causing the appearance of overcompensation in the following year.

In a large-scale comparison of 236 studies on effects of grazing on production, 17% of the studies had positive values for the effects of grazing on above-ground production, which were mainly grasslands with low-intensity grazing (Milchunas and Lauenroth 1993). The amount of overcompensation was usually small and based on measurements of ISC or even peak standing crop. When the data would have been corrected for senescing biomass, overcompensation might have been a rarer phenomenon.

To avoid the problem of senescing leaves, either ABP can be measured, or ISC can be corrected when the senescence flux is measured separately. Apart from measuring leaf demography and elongation, this can be done by removing and weighing dead leaves frequently in fixed plots. This is described by Davies (1981). ISC cannot be corrected by adding the standing dead pool at the end of the experiment to the production. Cargill and Jefferies (1984) showed that standing dead can be constant throughout the growing season. Kotanen and Jefferies (1987) and Bazely and Jefferies (1989) showed that at the same time, still a considerable flux of senescing leaves can be found. So not all leaves that have died can be found in the standing dead pool. In Yellowstone National Park (USA) overcompensation was demonstrated by comparing the peak standing crop of ungrazed plants with the summed increments in standing crop in temporary exclosures (Frank and McNaughton 1993). In this study the authors assume that senescence of leaves is negligible, because the standing dead pool is very small. However, shoot dynamics should be quantified to make reliable assumptions about fluxes in a growing sward.

Making the intervals shorter by clipping plots more frequently is no solution for the described problem using ISC to determine production. The basis for the problem is not in the absolute amount of biomass that died during an interval, but in the ratio between senescing and newly produced biomass, which is not affected by making the intervals shorter. The four methods to measure net primary productivity proposed by McNaughton et al. (1996) avoid problems with variable growth rate and variable grazing intensity, but they do not solve the problem of senescing biomass. To achieve accurate measures, a correction for senescing biomass should be added.

In our study, we conclude that there is no overcompensation following grazing by barnacle geese. On the tundra of Bylot Island, Canada, Gauthier et al.

(1995) also found no overcompensation after grazing by greater snow geese, while on the saltmarsh of La Pérouse Bay, Canada, grazing of lesser snow geese did cause overcompensation (Cargill and Jefferies 1984), even after correction for senescing leaves (Appendix). Why is overcompensation not found in our study? In La Pérouse Bay, the beneficial effect of utilization by geese is attributed to the fertilizing effect of nutrients from goose droppings. Bazely (1988) suggested that similar results would have been obtained in a study in Greenland (Madsen and Mortensen 1987) if the fertilizing effect of droppings was taken into account. However, intensity of grazing determines the magnitude of overcompensation (Hik and Jefferies 1990) and variation in grazing intensity between various studies could account for variation in compensatory growth (Madsen 1988). Secondly, nutrients that leach from goose droppings do not benefit grasses directly in our study area. Most of these nutrients are taken up by mosses. Only a fourfold increase of dropping density could increase production (Loonen unpubl.). In the areas where overcompensation is measured at La Pérouse Bay, there is no dominance of mosses. Here the nutrients might directly benefit the grasses. Gauthier et al. (1995) also noted this nutrient uptake by mosses on Bylot Island and gave the absence of mosses as an explanation for the difference between his study on Bylot Island and La Pérouse Bay.

In this article, we wanted to demonstrate solely the effect of senescing leaves on the determination of overcompensation. For an exact determination of overcompensation, the duration of the experiment is important (Oosterheld and McNaughton 1991, Wegener and Odasz 1997). Below-ground biomass, shoot turnover and individual plant turnover should also be taken into account.

Conclusion

Poa arctica did not overcompensate for losses due to grazing. Measuring production with senescing leaves included or excluded causes a large difference in the results of studies investigating overcompensation. Grazed leaves contribute less biomass to the senescence flux than ungrazed leaves. Therefore, production of ungrazed swards is more seriously underestimated than production of grazed swards when increment in standing crop is measured. In this way, the effect of grazing on changes in standing crop can be erroneously judged as overcompensation.

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Appendix. Recalculations of overcompensation from published data of La Pérouse Bay

This appendix contains the formulas which are used to estimate the Above-ground Biomass Production (ABP) from published data on Increment in Standing Crop (ISC), which are collected in La Pérouse Bay. In these papers ISC is referred to as Net Above-ground Primary Production (NAPP). The result of applying the formulas is a value for overcompensation based on ABP. The abbreviations used in the formulas are explained below.

Abbreviations

| | |
|-------------|-----------------------------------|
| LEL | = Life Expectancy of Leaves |
| gr. | = grazed |
| ungr. | = ungrazed |
| excl. | = enclosure |
| temp. excl. | = temporary enclosure |
| ISC | = Increment in Standing Crop |
| ABP | = Above-ground Biomass Production |
| C | = Consumption |
| StCrop | = Standing Crop |
| LD | = Leaf Deaths |

Formulas

$$\Delta\text{StCrop} = \text{StCrop}_{\text{end}} - \text{StCrop}_{\text{initial}}$$

$$\text{ISC} = \Delta\text{StCrop} \quad \text{if } \Delta\text{StCrop} > 0^1$$

$$\text{ISC} = 0 \quad \text{if } \Delta\text{StCrop} < 0^1$$

$$\text{LD} = \text{StCrop}_{\text{initial}} \times \Delta t(\text{days}) / \text{LEL}$$

$$\text{ABP} = \Delta\text{StCrop} + \text{LD} + \text{C}$$

Table A1. Life expectancy of leaves from different treatments in La Pérouse Bay. Data on *Carex subspatheae* from Kotani and Jefferies (1987: 968), data on *Puccinellia phryganodes* from Bazely and Jefferies (1989: 818).

| | <i>Carex</i> | <i>Puccinellia</i> |
|--|--------------|--------------------|
| LEL _{gr.} | 33 | 31 |
| LEL _{ungr.} | 46 | 36 |
| LEL _{temp.excl.} ² | 46 | 36 |

² Assumption: LEL_{temp.excl.} = LEL_{ungrazed}. Because LEL of leaves that appeared just after placing an enclosure in La Pérouse Bay did not differ from LEL of leaves that appeared later in the ungrazed treatment (Kotani and Jefferies 1987: 968), we assume that LEL in a temporary enclosure does not differ from LEL in a full season enclosure.

¹ With this widely used formula, assuming the production to be zero when negative production values are found, the phenomenon of senescing biomass is half recognised: it is senescing biomass which causes the negative production values, but it is only corrected for when those negative values actually occur.

Table A2. Biomass dynamics of *Carex subspathacea* in g m⁻² as calculated from Cargill and Jefferies (1984: Figs. 2b, 3b) LD = leafdeaths, C = consumption.

| Grazed | | | | | Ungrazed | | | Temporary enclosure | | |
|------------|----------|-----------|----|----|----------|-----------|----|---------------------|-----------|----|
| Date | St. crop | ΔSt. crop | LD | C | St. crop | ΔSt. crop | LD | Date | ΔSt. crop | LD |
| 31 May | 14 | | | | 17 | | | 17 May | | |
| 13 Jun. | 18 | 4 | 6 | 2 | 23 | 6 | 5 | 7 Jun. | 3 | 6 |
| 27 Jun. | 23 | 5 | 8 | 12 | 33 | 10 | 7 | 3 Jul. | 36 | 8 |
| 11 Jul. | 28 | 5 | 9 | 20 | 57 | 24 | 10 | 25 Jul. | 38 | 12 |
| 1 Aug. | 29 | 1 | 18 | 40 | 68 | 11 | 26 | 14 Aug. | 8 | 13 |
| 17 Aug. | 18 | -11 | 14 | 8 | 53 | -15 | 24 | 26 Aug. | 8 | 5 |
| Cumulative | | 4 | 55 | 82 | | 37 | 71 | | 93 | 44 |

Table A3. Biomass dynamics of *Puccinellia phryganodes* in g m⁻² as calculated from Cargill and Jefferies (1984: Figs. 2c, 3a) LD = leafdeaths, C = consumption.

| Grazed | | | | | Ungrazed | | | Temporary enclosure | | |
|------------|----------|-----------|-----|----|----------|-----------|-----|---------------------|-----------|-----|
| Date | St. crop | ΔSt. crop | LD | C | St. crop | ΔSt. crop | LD | Date | ΔSt. crop | LD |
| 28 May | 38 | | | | 38 | | | 17 May | | |
| 7 Jun. | 35 | -3 | 11 | 1 | 49 | 11 | 11 | 8 Jun. | 11 | 23 |
| 20 Jun. | 40 | 5 | 15 | 12 | 60 | 11 | 18 | 3 Jul. | 27 | 24 |
| 6 Jul. | 59 | 19 | 21 | 22 | 73 | 13 | 27 | 31 Jul. | 24 | 44 |
| 21 Jul. | 64 | 5 | 28 | 28 | 91 | 18 | 30 | 15 Aug. | 27 | 25 |
| 8 Aug. | 56 | -8 | 37 | 19 | 75 | -16 | 46 | 26 Aug. | 9 | 17 |
| 24 Aug. | 58 | 2 | 29 | 0 | 80 | 5 | 33 | | | |
| Cumulative | | 20 | 142 | 82 | | 42 | 164 | | 98 | 134 |

Standing crop was estimated from Cargill and Jefferies (1984). Leafdeaths are calculated from the average Life Expectancy of Leaves (LEL) from Kotanen and Jefferies (1987) and Bazely and Jefferies (1989), given in Table A1. Consumption is estimated from goose droppings using a digestibility of 34% (Cargill and Jefferies 1984: Table 2 and p. 678). Data were collected at various dates, but fitted in the intervals in which standing crop was measured (Tables A2 and A3).

Overcompensation

Using the published data, overcompensation is calculated traditionally as follows:

$$\text{Overcompensation}_{\text{ISC} - \text{temp.excl.}} = (\text{ISC}_{\text{temp.excl.}} / \text{ISC}_{\text{ungr.}}) \times 100\%$$

Recalculating the data reveals two methods to estimate overcompensation expressed in ABP: (a) using values from a grazed sward, including the amount consumed:

$$\begin{aligned} \text{Overcompensation}_{\text{ABP} - \text{grazed sward}} &= (\Delta\text{StCrop}_{\text{gr.}} + \text{LD}_{\text{gr.}} + \text{C}) / (\Delta\text{StCrop}_{\text{ungr.}} + \text{LD}_{\text{ungr.}}) \\ &\times 100\% \end{aligned}$$

(b) using values from temporary enclosures to estimate production in grazed swards:

$\text{Overcompensation}_{\text{ABP} - \text{temp.excl.}}$

$$= (\Delta\text{StCrop}_{\text{temp.excl.}} + \text{LD}_{\text{temp.excl.}}) / (\Delta\text{StCrop}_{\text{ungr.}} + \text{LD}_{\text{ungr.}}) \times 100\%$$

For *Carex subspathacea* (Table A2), the following values can be calculated:

$$\begin{aligned} \text{Overcompensation}_{\text{ISC} - \text{temp.excl.}} &= (93/51) \times 100\% \\ &= 182\% \end{aligned}$$

$\text{Overcompensation}_{\text{ABP} - \text{grazed sward}}$

$$= (4 + 55 + 82) / (37 + 71) \times 100\% = 131\%$$

$\text{Overcompensation}_{\text{ABP} - \text{temp.excl.}}$

$$= (93 + 44) / (37 + 71) \times 100\% = 127\%$$

For *Puccinellia phryganodes* (Table A3), the values are:

$$\begin{aligned} \text{Overcompensation}_{\text{ISC} - \text{temp.excl.}} &= (98/58) \times 100\% \\ &= 169\% \end{aligned}$$

$\text{Overcompensation}_{\text{ABP} - \text{grazed sward}}$

$$= (20 + 142 + 82) / (42 + 164) \times 100\% = 118\%$$

$\text{Overcompensation}_{\text{ABP} - \text{temp.excl.}}$

$$= (98 + 134) / (42 + 164) \times 100\% = 113\%$$