

Phenological changes within a growth season in two semi-natural pastures in southern Sweden

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Phenological changes within a growth season were investigated in two grazed, semi-natural grasslands in southern Sweden. On four occasions during the growth season, two independent observers recorded plant frequency and percentage cover. The vegetation data sets were analysed with ordination methods. The temporal changes were highly significant, but accounted for only a small part of the total variation in the data. Most species had early maxima, regarding both cover and frequency. There were differences in temporal pattern between the two grasslands. In a xeric area, the vegetation underwent a major change sometime in August, between survey-visit three and four. In a mesic area, the vegetation changed throughout the study period but least so during August. Therefore, phenological changes can be manifested in different ways, even within the same geographic region. Species-wise ordination scores highlighted those species whose records might be most affected by phenological patterns, information which is valuable when evaluating data collected in Scandinavian grasslands.

Key words: grassland, grazing, management, phenology, PCA, RDA, Sweden

Introduction

In northern Europe today, most of the old meadows and pastures have been turned into arable land or been overgrown by forest (Hæggström 1983, Persson 1984, Losvik 1988, Skånes 1990, Bengtsson-Lindsjö *et al.* 1991, Huhta & Rautio 1998). In order to preserve the remaining species-rich meadows and pastures, it is important to understand their ecology. One relatively unstudied phenomenon is the fact that the abundance of plant species changes within the growth season

(Kirby *et al.* 1986, Thóralldóttir 1990, Losvik 1991, McCarthy *et al.* 2001, Small & McCarthy 2002). As vegetation-monitoring data are often collected without necessarily taking into consideration the time of the growth season, phenological changes will always be manifested in the data and therefore will potentially affect their interpretation. For example, differences between sites might partially depend on the fact that data were collected on different dates (Hope-Simpson 1940, Kirby *et al.* 1986). Furthermore, the same calendar dates in different years might not be

comparable due to weather differences (Stampfli 1992). Therefore, the interpretation of vegetation data might benefit from knowledge of the magnitude of such phenological changes, and information highlighting those species exhibiting the largest and smallest changes.

The purpose of this study was to use multivariate statistical methods to evaluate the temporal trends in species-rich grasslands after covarying out spatial patterns. To reduce inter-observer differences, two persons made independent records (Nilsson 1992). For a more detailed appreciation of the temporal changes, the vegetation was described with plant-cover estimates as well as a subplot-frequency method.

Materials and methods

Study sites

Two semi-natural grasslands grazed by cattle were selected in the county of Östergötland, south-eastern Sweden. The sites chosen were in the nature reserves Åsabackarna (58°17'N, 14°55'E) and Solberga (58°21'N, 15°12'E).

The area within Åsabackarna where the study took place is a xeric, species-rich pasture on relatively coarse, glaciofluvial deposits, influenced by nearby limestone. It is the highest point in the reserve and is sparsely wooded with *Picea abies*, *Juniperus communis* and *Rosa dumalis*. The area has probably been grazed for several hundreds of years (D. Nilsson, County Administrative Board of Östergötland, pers. comm.). To estimate the stocking density, both in the actual study year and that preferred for nature conservation purposes in southern Sweden, we used the calculation method of Ekstam and Forshed (1996). At Åsabackarna, the actual values and the recommended ones were 0.49 and 1.33 cattle units ha⁻¹, respectively.

Solberga nature reserve consists of a mosaic of wooded, hilly pastures on glaciofluvial deposits. The studied areas in the reserve were two pastures situated on the slopes of the river Svar-tån. The conditions are mesic and *Quercus robur*, *Betula* spp., *Pinus sylvestris*, *Tilia cordata*, *Alnus* spp., *Juniperus communis* and *Rosa dumalis* were the dominating trees and shrubs. Solberga,

which was earlier a meadow, has a denser vegetation cover compared with Åsabackarna. The actual stocking density at Solberga during the study year differed between the two pastures: 2.89 vs. 1.26 cattle units ha⁻¹ (the recommended value, according to Ekstam and Forshed (1996), was 1.50 cattle units ha⁻¹ at both pastures).

The mean temperature from May to August during the study year was above the 30-year average (SMHI 2002a, 2002b, 2002c, 2002d). The precipitation was above the monthly long-term average during May, June and July, but below during August (SMHI 2002a, 2002b, 2002c, 2002d).

Data collection

Within each of the nature reserves, eight permanent plots were marked using 20-cm-long underground iron rods. Trees, large rocks and fence posts were recorded as 'fixed' points and used, together with a metal detector, to relocate the plots. The plots were placed so as to cover the variation within the pasture. Paths, large rocks, shaded and wet areas were avoided. In Solberga, however, some plots were shaded for parts of the day.

The sites were visited four times from May to August in 2002. The first visit was 23 May–7 June, the second 24 June–1 July, the third occasion 29 July–1 August, and the fourth 26–29 August.

The species were recorded using two different methods: frequency analysis and percentage cover (Ekstam & Forshed 1996). Using a wooden 0.5-m² frame divided into 25 squares, the frequencies of the different species were recorded. Frequency was only noted when a species was rooted in a subplot. The percentage of cover was noted on a continuous percentage scale using the same 0.5-m² frame.

Two independent observers conducted the same inventories, and mean values for each species were calculated from the data of both observers (except for a few cases when a species had been missed by one of the observers).

The plants were identified to species level whenever possible. Mosses, lichens, rocks and bare soil were 'lumped' together and noted as

cover, but not frequency. Although grasses make up an important part of grassland vegetation, the many species involved make it time-consuming to identify all the non-flowering grasses to species level, especially when using a subplot-frequency method. Grasses and sedges were therefore not identified but placed into a common category, “grasses/sedges”, except for *Luzula* spp.

Species difficult to identify or distinguish were merged into groups, even if they could easily be distinguished later in the season (Appendix). This means that the number of species recorded and the total variation in the data is somewhat lower than in conventional vegetation data from similar grasslands.

Data analysis

The data were first analysed using detrended correspondence analysis, DCA, to find out whether a linear or unimodal analysis should be used. Since the purpose of this study was to investigate the phenological changes between the different inventory periods, the plot identity was used as a number of categorical covariables in order to eliminate the plot differences. Hence, a partial DCA (pDCA) was calculated, combining data from the two sites. For all analyses of percentage cover, the species data were square-root transformed, in order to dampen the influence of the relatively few species with high percentage cover. The unspecified groups “unidentified” and “mosses, lichen, rocks & soil” were made supplementary, i.e. they did not influence the ordination, but their position in ordination space could be calculated afterwards.

For the frequency analysis, the maximum length of gradients was found to be 3.40 SD and for percentage cover 3.62 SD. This indicated a relatively short gradient in the data and a linear method was preferred (ter Braak & Prentice 1988, Lepš & Šmilauer 2003). Therefore, partial redundancy analysis, pRDA was used to analyse the phenological difference between the different periods of inventory, using the combined data from the two sites. As “time” was treated as a single continuous variable, using Julian day number, this resulted in a single constrained axis in the pRDA. The strength of the pRDA was

evaluated in a Monte Carlo test with 9999 unrestricted permutations.

As the pRDA assumed a linear change over time, an assumption not necessarily appropriate, a second set of analyses was conducted with principal component analysis (PCA). In this case, samples are sorted based on species composition only. The sites were analysed separately, using plot identity as covariables, i.e. partial PCA (pPCA) were conducted. Initial pDCA had shown that the maximum lengths of gradients in these data sets were short (0.8–1.4 SD), indicating the appropriateness of using a linear method.

For the statistical analyses CANOCO 4.5 was used (ter Braak & Šmilauer 2002).

Results

The total number of taxa recorded in the two pastures on the first, second, third and fourth inventory visits were 75, 74, 64 and 59, respectively, with the cover method, and 75, 77, 69 and 65 with the frequency method. Hence, there was a decreasing trend in the number of species found during the growth season.

pRDA analyses

There was a clear, significant change in vegetation composition during the growth season. The pRDA was highly significant for both the frequency data ($F = 11.234$, $p = 0.0001$) and the percentage cover data ($F = 4.143$, $p = 0.0001$). The variation explained by time in the pRDAs was slightly larger for the frequency data than for the cover data: 1.7% and 1.1% respectively.

Most of the species were found early in the inventory series and only a few showed up later (data not shown). Ordination scores indicated an early maximum, for example, for: *Rhinanthus minor*, *Anemone nemorosa*, *Saxifraga granulata*, *Cerastium fontanum/semidecandrum* and *Platanthera* sp. Among those that had their maximums later in the season were *Ajuga pyramidalis*, *Cirsium acaule*, *Prunella vulgaris*, *Hypericum maculatum* and *Veronica officinalis* (Appendix).

Inspecting the ordination scores, the impression is that most species had their maximum

frequency and maximum cover at about the same time during the growth season (similar ordination scores using both frequency and cover data). Exceptions were, for example, *Taraxacum* spp., *Viola hirta*, *Luzula* spp., grasses/sedges and *Achillea millefolium*, whose frequency seemed to peak before their cover (as judged by the differences in ordination scores; see Appendix). In contrast, some species had their highest cover earlier than they had their highest frequency, e.g. *Cerastium fontanum/semidecandrum* (Appendix). Maybe the most surprising item was the category “mosses, lichens, rocks & soil”, which appeared to have its highest cover later in the season, as did the category “unidentified” (Appendix).

pPCA analyses

Åsabackarna

The results from plant frequency, as well as plant cover data, indicated that the vegetation underwent a major change sometime during August (between visits three and four) in the Åsabackarna pasture (Fig. 1). Interestingly, the species that contributed most to this pattern in the two data sets were not the same. *Prunella vulgaris* and grasses/sedges had increased most at the last survey, in frequency and cover, respectively (Fig. 1). Many more species had decreased (long arrows pointing in the direction away from the last survey) than increased: for example, *Ranunculus* spp. in both data sets, *Taraxacum* for frequency and *Veronica* spp. for cover (Fig. 1). Early species were *Veronica* spp., *Geranium pusillum* and *Cerastium fontanum/semidecandrum*, as judged by their frequency (Fig. 1a); cover data also highlighted these same early species, in addition to *Saxifraga granulata*, *Primula veris* and *Myosotis* spp. (Fig. 1b).

Solberga

The results from plant frequency, as well as plant cover data, indicated that the largest temporal changes at Solberga were from the first, via the second, through to the other two visits (Fig. 2). Hence, in contrast to Åsabackarna, there was not

much change during August at Solberga. Species that decreased during the growth season were *Anemone nemorosa* and *Platanthera* sp. (both methods, Fig. 2), *Trollius europeaus* and *Lathyrus linifolius* (frequency, Fig. 2a), and *Rhinanthus minor* and *Saxifraga granulata* (cover, Fig. 2b). Late species were *Ajuga pyramidalis* and *Veronica* spp. (frequency, Fig. 2a) and *Plantago media* (cover, Fig. 2b).

Discussion

It is a well-known fact that vegetation changes during the course of a growth season (e.g. Kirby et al. 1986, Kennedy & Addison 1987, Small & McCarthy 2002, Aguilar et al. 2003). Such changes can be caused by some species that exploit only a part of the growth season. This is not, however, the main reason for the temporal pattern in grasslands dominated by perennial life forms, as was the case in the present study. Here, as elsewhere, most of the variation was accounted for by changes in abundance rather than to the appearance/disappearance of species. Therefore, what is important in our type of grassland is the timing of the peak of above-ground biomass. This in turn is modified by the removal rate through grazing or mowing.

The magnitude of the phenological changes detected in the present study was relatively modest: only 1%–2% of the variation in the data.

The overall phenological changes

The overall pattern of the pRDA (Appendix) was that most of the species had their maximum cover and frequency early in the growth season. Furthermore, the number of species recorded per survey visit decreased during summer. This would speak in favour of field studies being conducted in early summer, i.e. late May–June, since later studies would then miss more species without contributing any extra ones. This is a recommendation many weeks earlier than a previous one based on studies in Sweden (Steen 1957). Our studies were located in different parts of southern Sweden and probably involved dif-

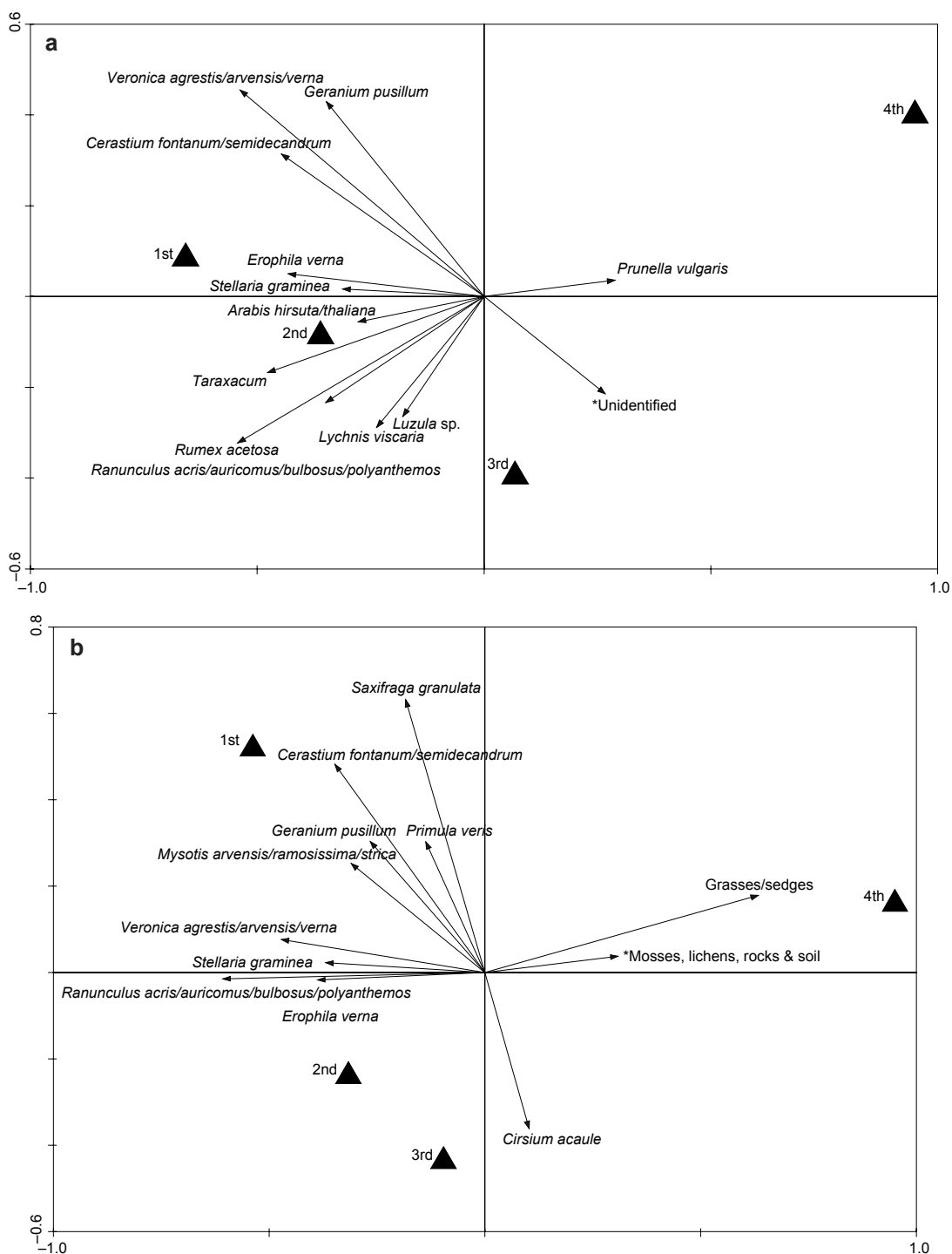


Fig. 1. pPCAs for the data from Åsabackarna. — **a:** Frequency data; Eigenvalues for PC1 and PC2: 0.040 and 0.022, respectively. Only the 13 species for which PC1 and PC2 explained most of the variation are indicated. — **b:** Cover data; Eigenvalues for PC1 and PC2: 0.027 and 0.016, respectively. Only the 12 species for which PC1 and PC2 explained most of the variation are indicated. *Supplementary category.

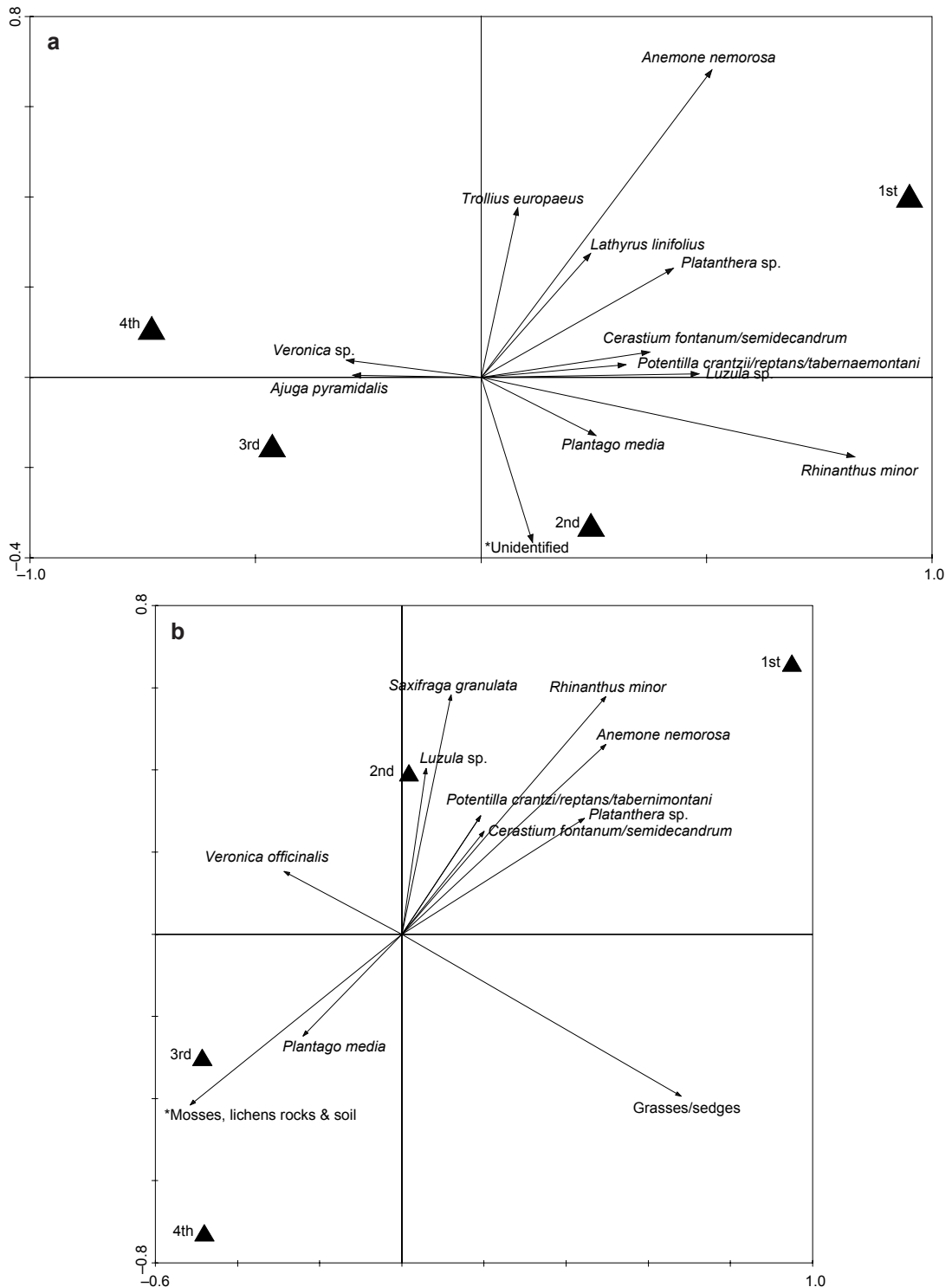


Fig. 2. pPCA for the data from Solberga. — **a:** Frequency data; Eigenvalues for PC1 and PC2: 0.060 and 0.014, respectively. Only the 12 species for which PC1 and PC2 explained most of the variation are indicated. — **b:** Cover data; Eigenvalues for PC1 and PC2: 0.048 and 0.032, respectively. Only the 13 species for which PC1 and PC2 explained most of the variation are indicated. *Supplementary category.

ferent stocking densities, which might explain our differing recommendations.

As expected, our data showed that vernal species, such as *Anemone nemorosa*, *Saxifraga granulata* and *Rhinanthus minor* (Lid 1985, Lid & Lid 1994), had their maximum frequency and maximum cover at the beginning of the study. However, other species, often thought of as “early species”, such as *Primula veris* and *Anemone pulsatilla* (Lid 1985, Lid & Lid 1994), did not have their maximum frequency and cover until somewhat later in the season (Appendix). It is worth pointing out that peak flowering does not necessarily coincide with peak biomass (as recorded by cover and frequency).

Some species also showed temporal differences between their frequency data and their cover data. For example, *Achillea millefolium* had a high frequency early on, but did not peak in percentage cover until later (Appendix). This is probably due to vegetative growth by rhizomes (Grime *et al.* 1988), increasing its cover but not its frequency during the growth season. *Achillea millefolium* has also been found to be a “late” species in other studies measuring its cover (Steen 1957, Losvik 1991). *Viola hirta*, which showed similar results as *A. millefolium* (Appendix), produces summer leaves that are much larger than the spring leaves (Grime *et al.* 1988), probably explaining why this species had a maximum cover later than maximum frequency. *Taraxacum* spp. showed differences between its frequency and cover data: it is reasonable to assume that there was not much recruitment during the season, but that the broad-leaved and continuously-growing *Taraxacum* sect. *Ruderalia*, in particular, should contribute to the increased percentage cover over time (Appendix).

One unexpected result was that the category “unidentified” seemed to increase as the season proceeded (Appendix). One might have expected the opposite, i.e. the number of unidentified specimens should be higher at the beginning of the study, when most species only had their vegetative parts developed and the observers were ‘untrained’ (still ‘getting their eye in’). Grazing by cattle may have contributed to the difficulty of identifying species later in the season. Since the number of unidentified species increased during

the season, our data again speak in favour of early fieldwork.

A possible reason why the category “mosses, lichens, rocks & soil” had increased by the fourth survey visit was the trampling and grazing by cattle, in combination with the low precipitation in August, which caused many herbs to desiccate.

Site differences

The pPCAs showed that the two sites differed not only in their species composition but also in the temporal pattern exhibited during the season (Figs. 1–2). In Solberga, the greatest changes occurred early (Fig. 2), while at Åsabackarna the greatest changes occurred late (Fig. 1). We suggest two possible explanations for these unexpected differences in temporal patterns: differing proneness to drought and differing levels of grazing intensity.

Weather data from the region showed that the study year was not an extremely dry or warm summer — only August had precipitation data lower than average (SMHI 2002a, 2002b, 2002c, 2002d), causing some drought. Xeric areas, such as Åsabackarna, are likely to be affected by drought to a greater extent than more mesic areas like Solberga. Grasses are drought-tolerant species and they are promoted following a warm and dry season (Dunnett *et al.* 1998). The small drought in August combined with the low grazing pressure at Åsabackarna probably caused the increase in the cover of grasses towards the end of our study. In Solberga, the grasses/sedges had their highest cover values early on and their decrease over time might be due to the relatively high grazing pressure at this site, perhaps combined with a temporal shift in where the cattle were preferentially grazing (personal observation).

Regional differences

Comparing the results from the current study with other similar studies conducted elsewhere, there are, as expected, some similarities in phenological patterns: for example, an increase in abundance towards the end of the season for *Prunella vulgaris* (Hope-Simpson 1940, Steen

1957). However, more striking are the differences. In the current study, *Ajuga pyramidalis* showed a clear maximum in both frequency and cover in the late part of the summer, whereas in a similar study in a mown sward in western Norway, with maritime climate, it had an early peak in May and thereafter dropped in frequency and cover (Losvik 1991). In a study in a grazed sward in Sweden, in a region with climate similar to that in our study area, there were no clear temporal patterns for this species (Steen 1957). In the Norwegian study, *Rumex acetosa* increased in cover towards the end of summer (Losvik 1991), whereas in the current study this species had a peak in both cover and frequency early in the season, a pattern similarly recorded in Sweden by Steen (1957). *Plantago lanceolata* was found to increase in frequency during the growth season in Britain (Hope-Simpson 1940), where climate is mild and the growth season long, but in the current study it had its highest frequency early in the season but increased in cover with time. In Norway, this species appeared to decrease in cover towards the end of the summer (Losvik 1991). *Plantago media* showed the same pattern as *P. lanceolata* in the British study (Hope-Simpson 1940), but in the present study it had an early peak, both in frequency and cover. *Cirsium acaule* was also found to have a varying phenology: in Britain it decreased in abundance from May to September (Hope-Simpson 1940) whereas in the current study it increased to a maximum in both frequency and cover towards mid-summer. *Leucanthemum vulgare* had its highest cover values at the end of June in Norway (Losvik 1991) compared with at the end of the present study.

All this taken together with the different temporal patterns between Åsabackarna and Solberga (see "Site differences" above) indicates differences in phenology between different species at various spatial scales. Differences between the phenology of different species from different locations can mean an additional source of variation in any vegetation data, possibly masking or enhancing inter-site differences. Furthermore, it is also likely that there are differences in temporal patterns at finer spatial scales, e.g. between individual sample plots within a grassland. Such variation will be lost when data

from several plots are merged.

There can be many reasons for the detected differences between regions and sites. There could be systematic, large-scale differences due to climate, resulting in plant species responding differently. It is also possible that, on larger scales, the same species exhibit different phenologies because of genotypic differences. On a smaller scale, the precipitation might be uneven and, especially the lack of rain, might hamper growth and therefore, possibly, also hinder temporal patterns in development (Stampfli 1992, Herben *et al.* 1995, Dunnett *et al.* 1998). Finally, it is apparent that the manifestation of phenological changes will be substantially modified by the removal of biomass. In contrast to mowing, grazing may be continuous and is often patchy and preferential (Wahlman & Milberg 2002). It is therefore obvious that the details of the management regime could influence the temporal dynamics (Steen 1957), e.g. fertilizer application, the presence and timing of mowing, the stocking density and start of grazing.

Conclusions

The results from this study showed that most species had their maximum frequency and cover early in the growth season. This implies that early field studies might result in more complete vegetation records than fieldwork conducted later in the growth season. Although there was a clear and significant change over time, "time" explained only a modest part of the total variation in data.

The two different study sites differed in their pattern of changes during the growth season. Such differences could possibly be due to the two sites having a different moisture status, as well as a different stocking density. These results serve to highlight that management and other site-specific variables influence the manifestation of a phenological pattern. Furthermore, when comparing the results from the current study, in southern Sweden, with similar studies on changes within one growth season from other regions, such as Norway (Losvik 1991), Great Britain (Hope-Simpson 1940) and central Sweden (Steen 1957), differences were found

in the phenology of several species. This may have further implications when plant community assessments from different regions, sites or points in time are compared, since phenological differences might mask or enhance inter-site differences.

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References

- Aguilar, V., Staver, C. & Milberg, P. 2003: Weed vegetation response to chemical and manual selective ground cover management in a shaded coffee plantation. — *Weed Res.* 43: 68–75.
- Bengtsson-Lindsjö, S., Ihse, M. & Olsson, E. G. A. 1991: Landscape patterns and grassland species diversity in the 20th century. — *Ecol. Bull.* 41: 388–396.
- Dunnett, N. P., Willis, A. J., Hunt, R. & Grime, J. P. 1998: A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. — *J. Ecol.* 86: 610–623.
- Ekstam, U. & Forshed, N. 1996: *Äldre fodermarker*. — Naturvårdsverkets Förlag, Stockholm.
- Grime, J. P., Hodgson, J. G. & Hunt, R. 1988: *Comparative plant ecology: A functional guide to common British species*. — Oxford Univ. Press, London.
- Hæggeström, C.-A. 1983: Vegetation and soil of the wooded meadows in Nätö, Åland. — *Acta Bot. Fennica* 120: 1–66.
- Herben, T., Krahulec, F., Hadincová, V. & Pecháčková, S. 1995: Climatic variability and grassland community composition over 10 years: separating effects on module biomass and number of modules. — *Functional Ecol.* 9: 767–773.
- Hope-Simpson, J. F. 1940: On the errors in the ordinary use of subjective frequency estimations in grassland. — *J. Ecol.* 28: 193–209.
- Huhta, A. P. & Rautio, P. 1998: Evaluating the impacts of mowing: a case study comparing managed and abandoned meadow patches. — *Ann. Bot. Fennici* 35: 85–99.
- Karlsson, T. 1998: Förteckning över svenska kärlväxter [The vascular plants of Sweden — a checklist]. — *Svensk Bot. Tidskr.* 91: 241–560. [In Swedish with English summary].
- Kennedy, K. A. & Addison, P. A. 1987: Some considerations for the use of visual estimates of plant cover in biomonitoring. — *J. Ecol.* 75: 151–157.
- Kirby, K. J., Bines, T., Burn, A., Mackintosh, J., Pitkin, P. & Smith, I. 1986: Seasonal and observer differences in vascular plant records from British woodlands. — *J. Ecol.* 74: 123–131.
- Lepš, J. & Šmilauer, P. 2003: *Multivariate analysis of ecological data using CANOCO*. — Cambridge Univ. Press, Cambridge.
- Lid, J. 1985: *Norsk, svensk, finsk flora*. 5th ed. — Det Norske Samlaget, Oslo.
- Lid, J. & Lid, D. T. 1994: *Norsk flora*. 6th ed. — Det Norske Samlaget, Oslo.
- Losvik, M. H. 1988: Phytosociology and ecology of old hay meadows in Hordaland, western Norway in relation to management. — *Vegetatio* 78: 157–187.
- Losvik, M. H. 1991: A hay meadow in western Norway: changes in the course of a growing season. — *Nordic J. Bot.* 11: 577–586.
- McCarthy, B. C., Small, C. J. & Rubino, D. L. 2001: Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. — *For. Ecol. Managem.* 140: 193–213.
- Nilsson, C. 1992: Increasing the reliability of vegetation analyses by using a team of two investigators. — *J. Veg. Sci.* 3: 565.
- Persson, S. 1984: Vegetation development after exclusion of grazing cattle in a meadow area in the south of Sweden. — *Vegetatio* 55: 65–92.
- Skånes, H. 1990: Changes in the rural landscape and impact on flora — a retrospective case study using aerial photographs. — *Geogr. Ann.* 72A: 129–134.
- Small, J. C. & McCarthy, B. C. 2002: Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. — *Plant Ecol.* 164: 37–48.
- SMHI 2002a: *Väder och vatten. Maj 2002* (5). — Sveriges Meteorologiska & Hydrologiska Institut, Norrköping.
- SMHI 2002b: *Väder och vatten. Juni 2002* (6). — Sveriges Meteorologiska & Hydrologiska Institut, Norrköping.
- SMHI 2002c: *Väder och vatten. Juli 2002* (7). — Sveriges Meteorologiska & Hydrologiska Institut, Norrköping.
- SMHI 2002d: *Väder och vatten. Augusti 2002* (8). — Sveriges Meteorologiska & Hydrologiska Institut, Norrköping.
- Stampfli, A. 1992: Year-to-year changes in unfertilized meadows of great species richness detected by point quadrat analysis. — *Vegetatio* 103: 125–132.
- Steen, E. 1957: Botanisk säsongsvariation i två naturbeten [Botanical seasonal variation in two natural pasture swards]. — *Kungliga lantbrukshögskolan och statens lantbruksförsök. Statens jordbruksförsök* 84. Stockholm. [In Swedish with English summary].
- ter Braak, C. J. F. & Prentice, I. C. 1988: A theory of gradient analysis. — *Adv. Ecol. Res.* 18: 271–317.
- ter Braak, C. J. F. & Šmilauer, P. 2002: *Canoco 4.5 reference manual and CanoDraw for Windows. User's guide to Canoco for Windows — Software for canonical community ordination (version 4.5)*. — Microcomputer Power, Ithaca, New York.
- Thórhallsdóttir, T. E. 1990: The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. — *J. Ecol.* 78: 884–908.
- Wahlman, H. & Milberg, P. 2002: Management of semi-natural grassland vegetation: evaluation of a long-term experiment in southern Sweden. — *Ann. Bot. Fennici* 39: 159–166.

Appendix. Ordination scores from pRDA on surveys of 16 plots (2 sites) on four occasions during the 2002 growth season. Data were collected both with a frequency method and as percentage cover, and the two data sets were analysed separately. The species list is sorted by the scores for the frequency analysis; a high score indicates an early maximum. Twelve species rare in the data set are not shown (< 6 in total sum of frequencies, or < 2 in total sum of cover). Totals of frequency data and percentage of cover data are shown (both with a maximum of 1600). Nomenclature follows Karlsson (1998).

	Ordination score: Frequency data	Ordination score: Cover data	Total sum of	
			frequency	cover
Eigenvalue of constrained ordination axis	0.0172	0.0106		
<i>Rhinanthus minor</i>	0.420	0.411	216	47.5
<i>Anemone nemorosa</i>	0.358	0.376	70.5	15.5
<i>Saxifraga granulata</i>	0.321	0.416	20.5	7.5
<i>Cerastium fontanum/semidecandrum</i>	0.284	0.402	246	43
<i>Platanthera</i> sp.	0.270	0.286	22	13
<i>Taraxacum</i> spp.	0.264	-0.0360	268	70
<i>Ranunculus acris/auricomus/bulbosus/polyanthemos</i>	0.260	0.310	759.5	163.5
<i>Veronica agrestis/arvensis/verna</i>	0.257	0.287	82.5	8.5
<i>Lychnis viscaria</i>	0.256	0.254	7	4
<i>Erophila verna</i>	0.256	0.282	17.5	4
<i>Luzula</i> spp.	0.254	0.0967	796.5	169.5
<i>Arabis hirsuta/Arabidopsis thaliana</i>	0.228	0.226	12	3
<i>Viola hirta</i>	0.223	-0.0188	20.5	7.5
<i>Rumex acetosa</i>	0.210	0.126	313.5	54
<i>Myosotis arvensis/ramosissima/stricta</i>	0.162	0.178	20	4.5
<i>Alyssum alyssoides</i>	0.161	0.0969	12	3
<i>Geranium pusillum</i>	0.156	0.158	45.5	29
<i>Arenaria serpyllifolia</i>	0.156	0.0729	135.5	27.5
<i>Primula veris</i>	0.156	0.0849	22.5	16.5
<i>Stellaria graminea</i>	0.134	0.175	137	18.5
<i>Trollius europaeus</i>	0.122	0.0939	11	32
<i>Potentilla</i> sp.	0.121	0.0983	10	7.5
<i>Lathyrus pratensis</i>	0.117	-0.0173	57	17.5
<i>Lathyrus linifolius</i>	0.114	0.113	252.5	74.5
<i>Campanula rotundifolia</i>	0.109	0.0080	345	58
<i>Anemone pulsatilla</i>	0.105	-0.0185	10	11
<i>Veronica chamaedrys</i>	0.0583	0.0243	227.5	46
<i>Achillea millefolium</i>	0.0571	-0.0441	825.5	232
<i>Astragalus glycyphyllos</i>	0.0569	0.0406	35.5	128.5
Grasses/sedges	0.0551	-0.0669	1599.5	1466.5
<i>Fragaria vesca/viridis</i>	0.0538	0.0748	410	121
<i>Pilosella officinarum</i>	0.0463	0.0359	488.5	205
<i>Veronica serpyllifolia</i>	0.0413	0.0000	16	6
<i>Plantago media</i>	0.0402	0.0160	128.5	91
<i>Aegopodium podagraria</i>	0.0388	0.0832	20.5	12
<i>Centaurea jacea/Knautia arvensis</i>	0.0378	0.0434	292.5	157
<i>Geranium sylvaticum</i>	0.0355	0.0162	23.5	32.5
<i>Pimpinella saxifraga</i>	0.0316	0.0619	593	156
<i>Anthriscus sylvestris</i>	0.0299	0.0388	26	9.5
<i>Potentilla argentea</i>	0.0295	0.0520	82.5	73.5
<i>Trifolium campestre</i>	0.0289	0.0569	89.5	37
<i>Ononis spinosa</i> ssp. <i>maritima</i>	0.0269	-0.0678	155	190.5
<i>Artemisia campestris/vulgaris</i>	0.0244	0.0113	100.5	41.5
<i>Vicia</i> spp.	0.0231	-0.0363	152	43.5
<i>Filipendula vulgaris</i>	0.0226	0.0610	378	110

Continues

Appendix. Continued.

	Ordination score: Frequency data	Ordination score: Cover data	Total sum of	
			frequency	cover
<i>Alchemilla</i> spp.	0.0196	0.0674	354	154.5
<i>Medicago lupulina</i>	0.0195	0.0237	56	23.5
<i>Galium</i> spp.	0.0194	−0.0211	215	62.5
<i>Hypochoeris maculata</i>	0.0188	0.0049	36	43.5
<i>Sedum acre</i>	0.0173	0.0192	185.5	59
<i>Trifolium medium/pratense/repens</i>	0.0152	−0.0247	980.5	398.5
<i>Polygala vulgaris</i>	0.0150	0.0546	421	99.5
<i>Trifolium arvense</i>	0.0135	−0.0603	33	44.5
<i>Viola canina/riviniiana</i>	0.0099	−0.0386	204	61.5
<i>Hieracium</i> sect. <i>Vulgata</i>	0.0081	0.0782	45	21.5
<i>Lotus corniculatus</i>	0.0081	−0.0410	309.5	62.5
<i>Plantago lanceolata</i>	0.0074	−0.0855	911.5	335
<i>Potentilla erecta</i>	0.0074	0.0053	263.5	80
<i>Equisetum pratense/sylvaticum</i>	0.0025	0.0201	22.5	18
<i>Vaccinium vitis-idaea</i>	−0.0017	0.0316	66	14
<i>Leontodon autumnalis</i>	−0.0022	−0.0484	28.5	7
<i>Leucanthemum vulgare</i>	−0.0032	0.0049	224	71.5
<i>Potentilla crantzii/reptans/tabernaemontani</i>	−0.0034	0.0040	242.5	100.5
<i>Antennaria dioica</i>	−0.0036	0.0146	78.5	106
<i>Satureja acinos</i>	−0.0065	0.0564	10.5	4
<i>Veronica officinalis</i>	−0.0220	−0.0460	122	43
<i>Hypericum maculatum</i>	−0.0274	−0.0755	152.5	68
<i>Prunella vulgaris</i>	−0.0323	−0.0633	217.5	71.5
<i>Cirsium acaule</i>	−0.0601	−0.102	26	47
<i>Ajuga pyramidalis</i>	−0.0609	−0.155	14	8
Unidentified*	−0.0807	−0.175	35.5	19
Mosses, lichen, rocks & soil*	—	−0.4508	—	658

*Supplementary categories not affecting the pRDA outcomes.