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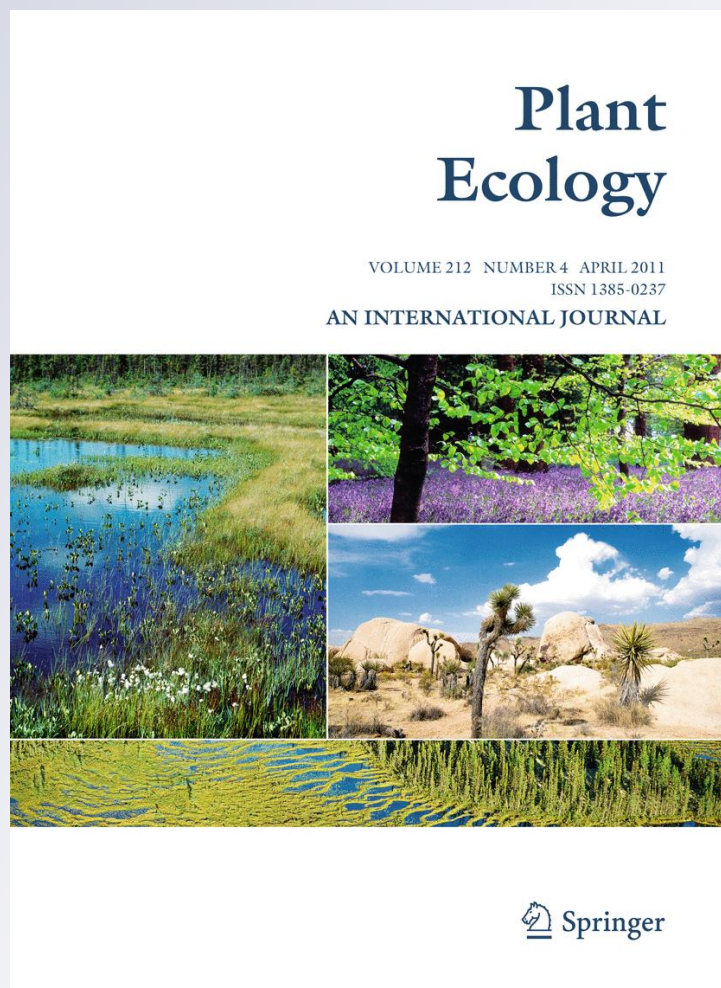
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# Geophytes–herbivore interactions: reproduction and population dynamics of *Anemone coronaria* L.

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**Abstract** *Anemone coronaria*, an attractive Mediterranean geophyte, seems to disappear from grazing-protected areas in Israel. We experimentally examined the ecological mechanism driving the decline of this geophyte. Ten plot-pairs were established, half we fenced as grazing exclosures and half were grazed by beef cattle. Grazing clearly reduced herbaceous biomass, increased relative solar photosynthetic active radiation (PAR) at ground level, but had almost no effect on soil properties. Grazing did not affect the number of flowers and young fruits produced by *A. coronaria*, nor the percentage fruit-set at the plot scale, indicating no effect on flowering, pollination, or on resource allocation to reproduction. Five years after grazing exclusion, *Anemone* seedling and adult plant densities were higher in grazed than in ungrazed plots. We propose a model explaining our results that can be applied also to other similar ecosystems: excluding grazing increased biomass and height of the herbaceous community and reduced relative PAR at ground level. Consequently, seedling, adult plant and flowering *Anemone* plant densities were lower in ungrazed plots. We recommend adding seasonal grazing as a management tool when vegetation outcompete light demanding geophytes that we wish to conserve.

**Keywords** Competition · Conservation · Grazing · Light · Livestock · Mediterranean

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## Introduction

Grazing by wildlife or domesticated animals is generally considered as a disturbance to grazed plants. According to Grime (1979), grazing is 'the total or partial destruction of plant biomass that arises from the activities of herbivores'. Others consider grazing as a stress factor restricting photosynthetic production (Dyer et al. 1993). Grazing, or its exclusion, has been recognized as a factor that can mould and shape plant community composition and structure (Crawley 1983; Todd and Hoffman 1999; Milchunas and Noy-Meir 2002). The contemporary approach considers abiotic conditions, competition and herbivory as prominent factors affecting community structure (Wardle and Barker 1997); this is especially valid in areas that have been exposed to heavy utilization by livestock for millennia (Perevolotsky and Seligman 1998). Heavy grazing may also affect ecosystem abiotic

characteristics (van der Koppel et al. 1997) such as erosion (Mwendra and Saleem 1997), soil structure (Proffitt et al. 1995) and productivity (Williams and Haynes 1995).

Grazing may have differing impacts on plant species due to herbivore preference or plant resistance (McIntyre et al. 1995; Dumont 1997: Lavorel et al. 1997). Perennial species, with long growing season, tall, erect or bulky structure, are preferred by grazers over small, prostrate species with short life cycle (Noy-Meir et al. 1989; Fernandez et al. 1993), and plants that develop chemical or morphological defence are grazed less than plants with less effective deterrents (Grubb 1992).

Geophytes are perennial herbaceous plants that shed their leaves during seasons unfavourable for growth (cold, dry), but resume growth from underground storage organs in the next season (Raunkiaer 1934). Tyler and Borchert (2002) suggest that geophyte diversity is highest in Mediterranean type ecosystems comprising 16% of the diverse Cape flora (Goldblat 1997) and 9% (217 species) of the Israeli flora (Fragman and Shmida 1997). Many geophytes in Israel are rare, considered sensitive to disturbance, and therefore require special conservation efforts. Following many years of traditional flower picking, geophytes with conspicuous flowers are now protected under Israeli law.

*Anemone coronaria* L. (Feibrun-Dothan and Danin 1991) is a geophyte with massive and attractive flowering during winter and early spring; it is common in open Mediterranean landscapes that are often used for livestock grazing (Koniak et al. 2009). *A. coronaria* in Israel is colour polymorphic, red flowers are most common (Shmida and Dafni 1989; Dafni et al. 1990), but white, pink, blue and violet flowers also occur in the same or different populations. Some of those populations served as stocks for *A. coronaria* cultivars grown in gardens (Horovitz et al. 1975a, b; Horovitz and Danin 1983). *A. coronaria* is largely avoided by mammalian herbivores, probably due to the toxins protoanemonin (Knight and Walter, 2001) and anemonin (Cheeke 1998) that gave the plant its scientific name. Currently, *A. coronaria* populations seem to decrease in grazing-protected areas but not in open rangelands in Israel.

Naveh and Whittikar (1979) were the first to observe a positive effect of grazing on geophyte diversity in Mediterranean plant communities in Israel. They suggested that grazing may release the light-mediated competitive inhibition of geophytes by their surrounding herbaceous vegetation, but did not present any supportive empirical data. An extensive correlative survey that monitored the relations between grazing exclusion and geophyte abundance in northern Israel demonstrated higher geophyte density in grazed than in neighbouring ungrazed sites (Noy-Meir and Oron 2001). In Israel, 107 geophyte species grow in open well-light Mediterranean habitats, whereas only 14 species grow in shady woodlands (Fragman and Shmida 1997), and negative effects of tree-shading on geophytes density (Hadar et al.1999) and flowering (Oz and Dafni 1991; Ne'eman 2003) were demonstrated by tree removal. However, no experimental study has examined the direct or indirect effects of grazing on a target geophyte in an herbaceous community, proposing and testing an ecological mechanism.

We hypothesized that grazing has a positive indirect effect on flowering, reproductive success and population density of *A. coronaria* by reducing the light-mediated competition with the surrounding herbaceous vegetation. To test this hypothesis we experimentally examined the effect of cattle grazing on the relationship between *A. coronaria* and its surrounding herbaceous vegetation. Specifically we asked: what is the effect of grazing on *Anemone* flowering, fruit-set, seedling, adult and flowering-plant densities, since these parameters determine the long-term persistence of the species in the community.

## Materials and methods

### Study area

This study was conducted at the Ramat Hanadiv Park, located at the southern tip of Mount Carmel in northern Israel, about 5 km from the Mediterranean sea-shore, at 150 m above sea level. The climate in the region is mild Mediterranean; the winter is short, wet and cool, and the summer is long, rainless and hot. Average annual rainfall is 600 mm, and it occurs mostly during November–March. Various formations of limestone and dolomite compose the bedrock in the park, and the common soil is Xerochreps, locally known as Terra-Rossa. The vegetation is a typical Mediterranean shrubland (also known as phrygana or

garrigue) dominated by the shrubs *Phillyrea latifolia* L., *Calycotome villosa* L. and *Pistacia lentiscus* L. and accompanied by *Sarcopoterium spinosum* L. Spach dwarf shrubs. Open patches of various sizes with herbaceous vegetation occur among the shrubs and this is the local habitat of *A. coronaria*.

Since 1985, the park has been committed to sustainable development and ecologically sound management. Four to six months of cattle grazing during January–June is regularly used to reduce herbaceous and woody biomass, as fire prevention management (Perevolotsky et al. 2003).

### Experimental design and measurements

In January 1997, we assigned ten pairs of experimental plots (2 × 3 m each) and fenced one of each plot-pair to exclude grazing. We monitored all *A. coronaria* plants in each plot every 10–14 days during the growing seasons (mid-December to mid-April, 1997–2002) counting the plants, the flowers, young fruits and fruits at seed dispersal stage per plant; we also recorded leaf length, flower and fruit–stem height. We measured the average height of the herbaceous vegetation in each plot and visually estimated its biomass (Tadmor et al. 1975); for calibration we harvested five quadrats (25 × 25 cm) outside the plots, dried the grass samples (3 days at 80°C) and weighed them. We did not remove any herbaceous vegetation from the exclosures during the experiment. The biomass estimates related only to the current-season green herbaceous vegetation. In addition, previous-year dry mulch comprised about 50% of the total standing biomass in January.

We measured solar photosynthetic active radiation (PAR) at ground level at noon on clear days using LI-COR (model LI-189); the average of three measurements represented each plot. To correct the differences in absolute radiation at different times and dates, we calculated the relative PAR (ground level/full sun). Three years after plot establishment we sampled the soil (0–5 cm) on three dates (27 Oct 1999, 12 Jan 2000 and 25 Feb 2000). Determination of water percentage at saturation, pH, conductivity (ds/m), N ($NO_3^-$ mg/l), P ($PO_4^{-3}$ mg/kg) and K ($K^+$ mg/l) were performed using standard methods at the Ministry of Agriculture regional laboratory. In spring 2001, 4 years after fencing, the densities of seedlings (plants with one leaf), adult plants (with

two or more leaves) and of flowering *A. coronaria* plants were measured.

### Statistical analyses

To reduce variations due to plot location, we designed the plots in pairs and used paired *t*-tests to compare variables between grazed and ungrazed plots, where we made several measurements of the same variable in one plot, and the plot average was used for further analyses. To examine differences among years we used repeated measures one-way ANOVA for the grazed and ungrazed plots separately. All variables that were proportions were transformed ($y$ = square root [arcsin(x)]) before analysis. We used SPSS 11.0.1 to analyze the data.

### Results

Exclusion of heavy cattle grazing for 3 years had no significant effects on soil pH, conductivity, P and K. Soil water capacity and N were lower under grazing only in one autumn sample (Table 1). Almost no differences were recorded in soil properties between the two winter samples (12 Jan 2000 and 25 Feb 2000) except for fivefold and tenfold increases in N in the grazed and ungrazed plots, respectively.

Grazing exclusion significantly affected the herbaceous vegetation. At the end of the 2000 grazing season, the herbaceous biomass outside of the exclosures was 82% less ($t_9 = 23.361$, $P < 0.001$) and its average height 92% lower ($t_9 = 14.566$, $P < 0.001$) than inside (Fig. 1A). Similar results were also obtained for both variables in all other years (not presented).

Relative PAR at ground level was on average 49.3% higher in gazed than in ungrazed plots during the whole season (January–June 2000) (Fig. 1B) and the differences were significant (e.g., on 11 Feb 2000: $t_6 = -10.003$, $P < 0.001$). In January, before the onset of the new-season growth and before the introduction of cattle, relative PAR in the ungrazed plots was already 33% lower than in the grazed plots (Fig. 1B) due to the effect of the dry herbaceous remains (mulch) from the previous growing season in the ungrazed plots.

Leaf petioles of *A. coronaria* were significantly longer by 41% ($t_4 = 6.499$, $P = 0.003$) in the

**Table 1** Average (±SE) percentage of water in saturated soil (Sat. %), pH, conductivity (Con.), $NO_3^-$ (N), $PO_4^{-3}$ (P) of soil samples (0–5 cm) in grazed and ungrazed plots

| Date | 27 Oct 1999 | | | 12 Jan 2000 | | | 25 Feb 2000 | | |
|---|---|---|---|---|---|---|---|---|---|
| Treatment | Grazed | Ungrazed | P | Grazed | Ungrazed | P | Grazed | Ungrazed | P |
| Sat. (%) | 82.17 ± 1.00 | 84.55 ± 1.17 | 0.037 | 84.98 ± 1.71 | 85.26 ± 2.36 | 0.893 | 84.85 ± 1.11 | ND | |
| pH | 7.19 ± 0.04 | 7.25 ± 0.05 | 0.193 | 7.63 ± 0.05 | 7.71 ± 0.05 | 0.168 | 7.53 ± 0.02 | 7.55 ± 0.02 | 0.443 |
| Con. (ds/m) | 0.67 ± 0.03 | 0.67 ± 0.02 | 0.921 | 0.516 ± 0.02 | 0.528 ± 0.01 | 0.600 | 0.62 ± 0.03 | 0.64 ± 0.02 | 0.395 |
| N (mg/l) | 1.26 ± 0.15 | 0.87 ± 0.04 | 0.002 | 7.09 ± 1.81 | 9.60 ± 1.53 | 0.162 | 2.28 ± 0.12 | 2.84 ± 0.32 | 0.512 |
| P (mg/kg) | 52.96 ± 2.80 | 57.28 ± 6.98 | 0.589 | 49.78 ± 3.51 | 71.73 ± 11.8 | 0.162 | 46.24 ± 1.24 | 48.15 ± 1.85 | 0.164 |
| K (mg/l) | 13.29 ± 1.31 | 13.10 ± 1.08 | 0.906 | 13.41 ± 0.79 | 14.85 ± 1.30 | 0.249 | ND | 14.85 ± 1.30 | |

$P$ = the significance of paired $t$-test, $n = 10$ for each pair, *ND* no data

ungrazed than in grazed plots. Stems of flowers, young fruits and fruits at seed dispersal were higher (by 26% ($t_4 = 5.536$, $P = 0.005$), 22% ($t_4 = 4.790$, $P = 0.009$) and 21% ($t_4 = 3.669$, $P = 0.021$), respectively) in the ungrazed than in the grazed plots (Fig. 2A). By the end of the 2000 season, grazing exclusion had affected neither the number of flowers per plant nor the number of young fruits per plant ($t_9 = -0.153$, $P = 0.882$ and $t_9 = 0.654$, $P = 0.529$, respectively), but the number of fruits at the dispersal stage was 52.5% higher ($t_9 = 3.793$, $P = 0.004$) in ungrazed than in grazed plots (Fig. 1C); similar results were obtained in all other years.

The fruit-set percentage was not different in grazed and ungrazed plots during the entire research period in 1997, 1998, 2000 and 2002 ($t_9 = 1.010$, $P = 0.339$; $t_8 = -0.230$, $P = 0.824$; $t_9 = 0.598$, $P = 0.565$ and $t_9 = 1.881$, $P = 0.093$, respectively), other than in 2001 when fruit-set was lower in grazed than in ungrazed plots by 22% ($t_8 = 3.397$, $P = 0.009$) (Fig. 2B).

During 1997, 1998 and 2000 there were no difference ($t_9 = -0.532$, $P = 0.608$; $t_9 = 0.582$, $P = 0.573$ and $t_9 = 1.713$, $P = 0.121$, respectively) in *A. coronaria* flowering-plant density in grazed and ungrazed plots (Fig. 2D). However, in 2001 and 2002 (after 4 years of grazing exclosure) *A. coronaria* flowering-plant density was higher in grazed than ungrazed plots ($t_9 = 2.863$, $P = 0.019$ and $t_9 = 2.636$, $P = 0.027$, respectively) (Fig. 2D). The effect of grazing exclusion on *A. coronaria* plant density was independent of the large and significant among year variation in flowering-plant density (range of 0.8–4.0 plants/m$^2$) in the various plots over the years ($F_{4,36} = 10.859$, $P < 0.001$ and $F_{4,36} = 4.252$,

$P = 0.006$, for ungrazed and grazed plots, respectively).

Finally, in 2002, following 5 years of grazing exclusion, *A. coronaria* seedling and adult plants densities were significantly lower in ungrazed than grazed plots, by 61.7% ($P = 0.054$) and 67.4% ($P = 0.035$), respectively (Fig. 2C).

## Discussion

Herbivory plays a central role in community dynamics. Yet, little empirical research has been carried out into the mechanisms through which grazing affects the complex relationship between a target plant and the community (Anderaon and Briske 1995). Grazing may directly affect plants by reducing their biomass or by trampling them and indirectly through alterations of soil properties. However, little attention has been paid to the indirect biotic effects of grazing through its negative effect on neighbouring plants, reducing their ability to compete for limited resources such as water, soil nutrients or light.

*Anemone coronaria* has developed three main adaptive mechanisms to cope with the intense competition from surrounding dense herbaceous vegetation: (1) Early-season growth and reproduction which precedes the massive growth of competing herbaceous vegetation in winter and spring, (2) Accumulation of reserves in a corm that enables the early growth and (3) Phenotypic plasticity, the ability of elongating leaf petioles, flower and fruit stems to keep above the herbaceous vegetation (Figs. 1a, 2a), allowing efficient photosynthesis, pollination and seed dispersal.

**Fig. 1 A** Seasonal changes between grazed (G) and ungrazed (NG) plots for: **A**. Average height (cm) and biomass (g m$^{-2}$) of herbaceous vegetation. **B** Average relative solar radiation (%) at ground level. **C** Average number of flowers per *A. coronaria* plant (Flw), young fruits (Frt) and fruits at seed dispersal (Disp) stage. For all panels $n = 20$, and the arrow indicates the commencement of grazing
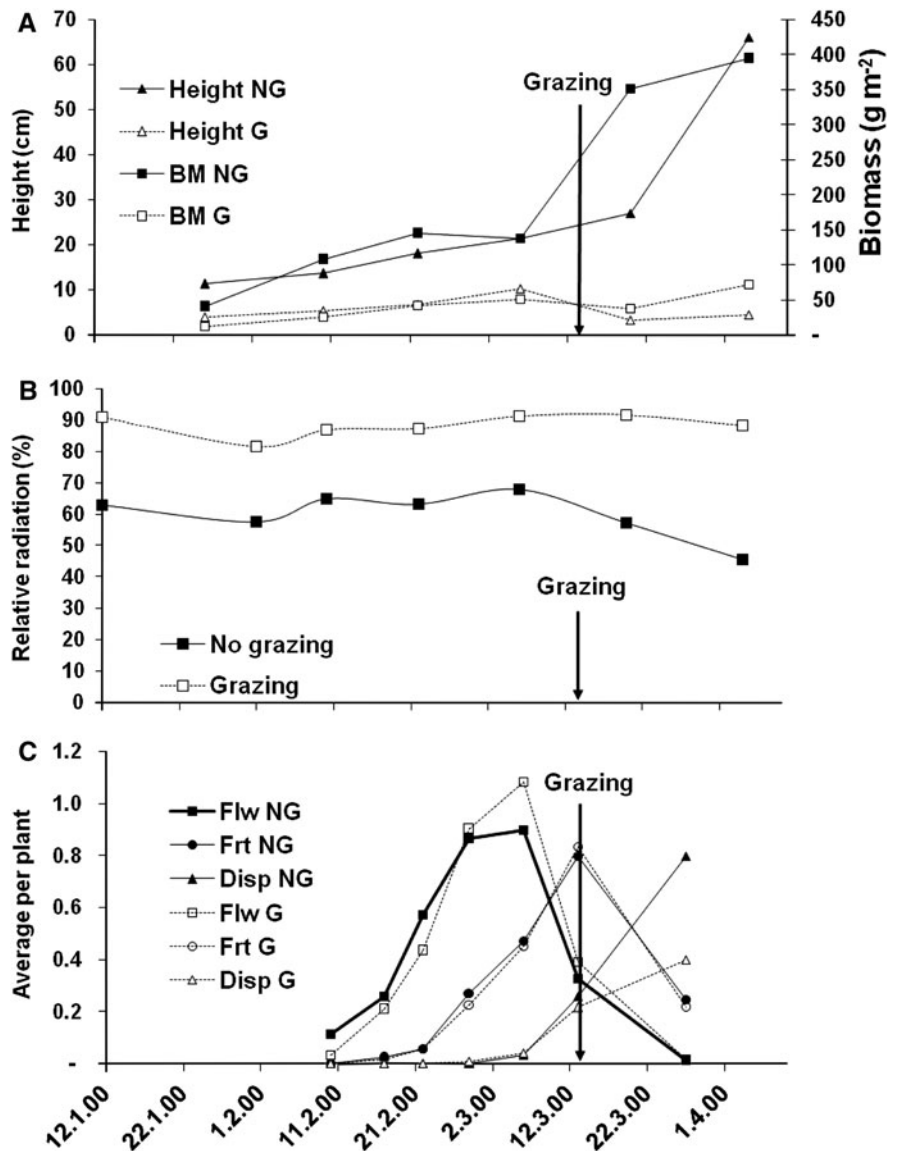


Grazing clearly affected herbaceous biomass and height in our plots (Fig. 1A), but not the number of flowers and young fruits produced by individual plants of *A. coronaria* (Fig. 1C), or the percentage fruit-set at the plot scale (Fig. 2B), indicating no effect of grazing on flowering, pollination or resource allocation to reproduction. However, grazing did negatively affect the number of fruits at seed dispersal stage, probably due to trampling (Fig. 1C).

The presence of secondary metabolites (Cheeke 1998; Knight and Walter 2001) explains the unpalatability and the minimal direct damage caused to *A. coronaria* by livestock grazing. In contrast, the reintroduced roe deer has been observed eating *A. coronaria* flowers (Wallach et al. 2009), but due to their low density in the park, the deer so far appear to have little or no impact on *A. coronaria* populations.

Grazing may have indirect effects on plants by alteration of soil properties, mainly its nutrient content (e.g., Polley and Detling 1989; Tilman 1990; Frank et al. 2000). Three years of grazing exclusion have had almost no effect on soil properties
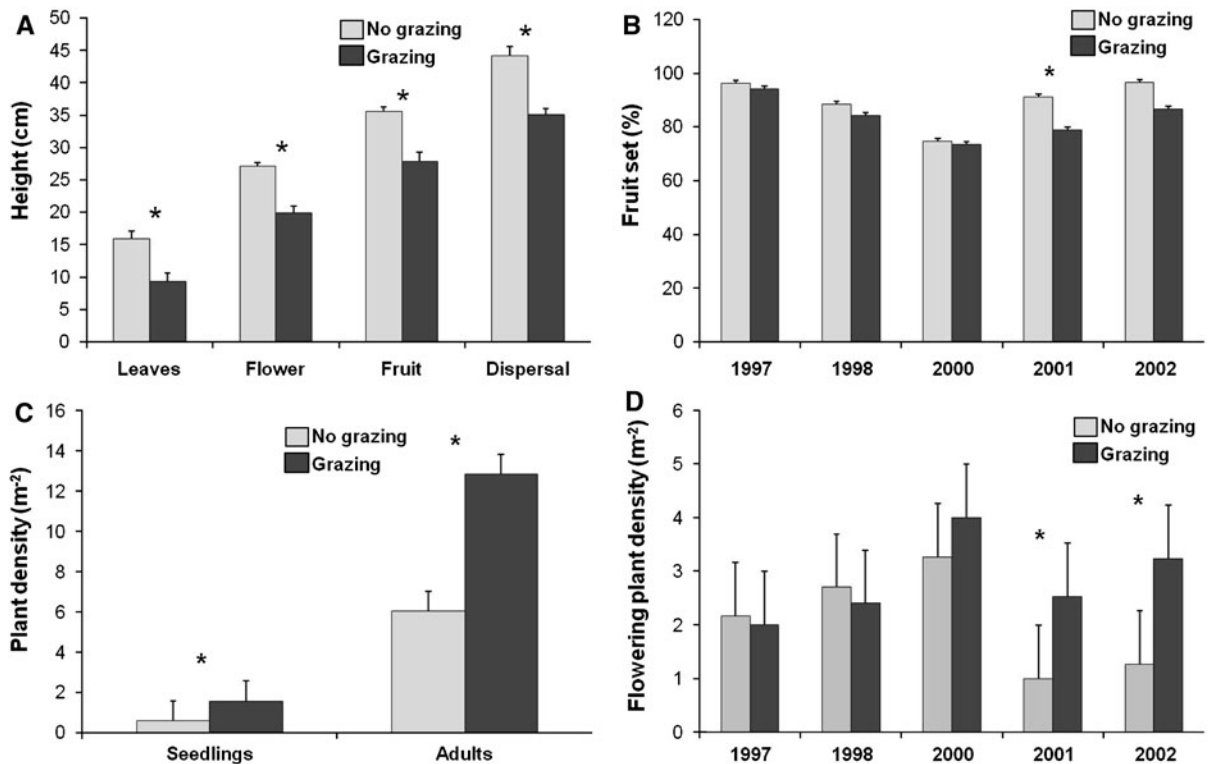
Fig. 2 **A** Average (±SE) leaf length (cm), and height (cm) of flowers, young fruits and fruits at seed dispersal of *A. coronaria*, in 2000, in grazed and ungrazed plots. **B** Annual average (±SE) fruit-set (%) in *A. coronaria* in grazed and ungrazed plots. **C** Annual average (±SE) density of *A. coronaria* adult plants and seedlings, in 2002, in grazed and ungrazed plots. **D** Annual average (±SE) density of flowering *A. coronaria* plants in grazed and ungrazed plots. For all panels asterisk indicates statistical significance ($P < 0.05$) in paired *t*-test, $n = 20$ for each pair

(Table 1). Therefore, it is not likely that grazing in an indirect way via soil nutrient content, positively affected *A. coronaria* seedling and plant density.

Grazing, and trampling, may affect plant community structure by creating new establishment gaps in a dense sward (Noy-Meir et al. 1989), or by reducing competition for limited resources such as light, soil nutrients, or moisture (Wardle and Barker 1997; Taylor et al. 1997; van der Wal et al. 2000). The main growing season of *A. Coronaria* is during the winter rainy season, thus competition for water seems unlikely.

Relative PAR at ground level (Fig. 1B), but not soil nutrients (Table 1) differed between grazed and ungrazed plots. Grazing reduced biomass and height of the current year's growth, in addition it also reduced the dry herbaceous remains (mulch) of the previous growing season, decreasing relative PAR at the onset of the growing season (Fig. 1B). We propose that by removing the previous year's mulch

and by further reducing current green herbaceous biomass grazing reduces shading and increases relative PAR at ground level. Optimal germination of *A. coronaria* occurs at 10–15°C in darkness and it is inhibited by far-red light (Horovitz et al. 1975a, b; Bullowa et al. 1975). Therefore, the additional light at ground level probably did not increase seed germination but rather the development and establishment of seedlings, resulting in higher seedling and adult plant densities (Fig. 2C), as well as the number of flowering plants in the grazed plots (Fig. 2D).

In a number of other ecosystems, geophytes also positively responded to better illumination due to grazing or fire, which stimulated their growth and flowering (Stone 1951; Tyler and Borchert 2002; Diadema et al. 2007; Gomes-Garcia et al. 2009). Our results are also in concert with studies of several other *Anemone* species. Litter removal increased light intensity and consequent germination and seedling density of *A. nemorosa*, a common plant of European

deciduous forests (Eriksson 1995; Holdergger 1996). Coppicing dramatically increased the flowering intensity of *A. nemorosa* (Mason and Macdonald 2002). Fertilization increased plant community biomass and caused consequent decrease in *A. parviflora* density (John and Turkington 1997). Other studies have found negative effects of grazing on geophytes (McIntyre et al. 1995; Lavorel et al. 1999; Dupre and Diekmann 2001), but it has been suggested that in these cases, the effect was mainly due to trampling-damage to underground storage organs. We found no such evidence for *A. coronaria*; moreover, wild boars (*Sus scrofa*) that are notorious in their digging in search of bulbs, ignored *A. coronaria* corms.

We propose a descriptive mechanistic model to illustrate the positive indirect effect of cattle grazing on *A. coronaria* (Fig. 3). In the absence of grazing, herbaceous biomass accumulates during the growing season and its remains turn into mulch that covers the soil surface from summer to the beginning of winter. As a result, the soil surface is partially shaded, which may have a negative effect on seedling growth and establishment, but not on seed germination. The additional shading created by the rapid growth of surrounding herbaceous vegetation in the absence of grazing induces elongation of leaf petioles, flower and fruit stems. The elongation of petioles and stems

does not contribute to photosynthesis, but probably decreases reserve accumulation in the corm. Reproductive success of geophytes is often positively correlated to corm or bulb size (Boeken 1989), and a decrease in corm reserves could therefore impair reproductive success in the following year. We propose this mechanism to explain the decrease in the density of *A. coronaria* seedlings, adult and flowering plants in our experimental ungrazed plots (Fig. 3). Fruit-set was high; we therefore assume that propagule pressure was similar in grazed and ungrazed plots. The lower *A. coronaria* seedling density in the ungrazed plots probably indicates that there was a decrease in seedling establishment in the ungrazed plots. We speculate that this is the result of the shady conditions at ground level (Fig. 3). In sum, it appears that *A. coronaria* density is limited mainly by light radiation reaching ground level, which is low in ungrazed areas due to shading caused by the surrounding herbaceous vegetation. By reducing herbaceous biomass, grazing increases light intensity that is needed for the establishment of *A. coronaria* seedlings.

Conservation in Mediterranean environments is often associated with active management (Perevolotsky 2006) aimed at controlling the effects of natural succession of the plant community in protected areas.

**Fig. 3** A mechanistic descriptive model of the indirect effects of livestock grazing on *A. coronaria* population density mediated by light radiation at ground level and consequent seedling establishment sites
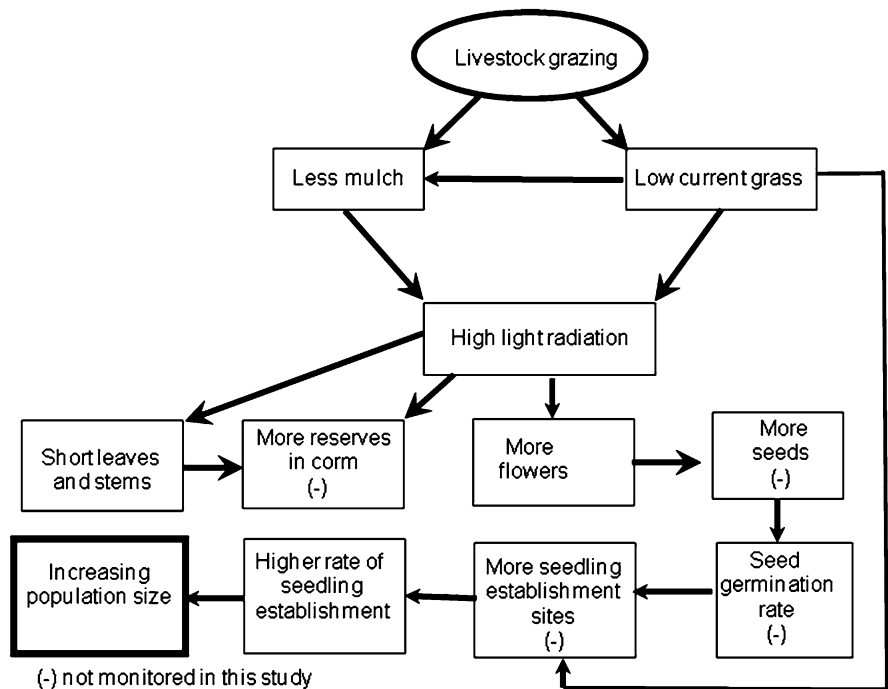
Based on the findings of this study and on the effect of fire on geophytes (e.g., Diadema et al. 2007), we recommend adding seasonal grazing or controlled burning to the conservation management tool-kit when neighbouring herbaceous or woody vegetation outcompete geophytes that we wish to conserve.

# References

Anderaon VJ, Briske DD (1995) Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? Ecol Appl 5:1014–1024

Boeken B (1989) Life histories of desert geophytes—the demographic consequence of reproductive biomass partitioning patterns. Oecologia 80:278–283

Bullowa S, Negbi M, Ozeri Y (1975) Role of temperature, light and growth regulators in germination in *Anemone coronaria* L. Austr J Plant Physiol 2:91–100

Cheeke PR (1998) Natural toxicants in feeds, forages and poisonous plants. Interstate Publishers, Danville

Crawley MJ (1983) Herbivory: the dynamics of animal–plant interactions. Blackwell, Oxford

Dafni A, Bernhardt P, Shmida A, Ivri Y, Greenbaum S, O'Toole C, Losito L (1990) Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. Isr J Bot 39:81–92

Diadema K, Medail F, Bretagnolle F (2007) Fire as a control agent of demographic structure and plant performance of a rare Mediterranean endemic geophyte. C R Biol 330: 691–700

Dumont B (1997) Diet preferences of herbivores at pasture. Ann Zootech 46:105–116

Dupre C, Diekmann M (2001) Differences in species richness and life-history traits between grazed and abandoned grassland in southern Sweden. Ecography 24:275–286

Dyer MI, Turner CL, Seastedt T (1993) Herbivory and its consequences. Ecol Appl 3:10–16

Eriksson H (1995) Seedling recruitment in deciduous forest herb: the effect of litter, soil chemistry and seed bank. Flora 190:65–70

Feibrun-Dothan N, Danin A (1991) Analytical flora of Eretz-Israel. Cana, Jerusalem

Fernandez AR, Laffarga JM, Ortega F (1993) Strategies in Mediterranean grassland annuals in relation to stress and disturbance. J Veg Sci 4:313–322

Fragman O, Shmida A (1997) Diversity and adaptation of wild geophytes along an aridity gradient in Israel. Acta Hortic 2:795–802

Frank DA, Groffman PM, Evans RD, Tracy BF (2000) Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park. Oecologia 123:116–121

Goldblat P (1997) Floristic diversity of the Cape flora of South Africa. Biodiv Cons 6:359–377

Gomes-Garcia D, Azorin J, Aguirre AJ (2009) Effects of small-scale disturbances and elevation on the morphology, phenology and reproduction of a successful geophyte. J Plant Ecol 2:1–13

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester

Grubb PJ (1992) A positive distrust in simplicity–lessons from plant defences and from competition among plants and among animals. J Ecol 80:585–610

Hadar L, Noy-Meir I, Perevolotsky A (1999) The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. J Veg Sci 10:673–682

Holdergger R (1996) Effects of litter removal on the germination of *Anemone nemorosa*. Flora 191:175–178

Horovitz A, Danin A (1983) Relatives of ornamental plants in the flora of Israel. Isr J Bot 32:75–95

Horovitz A, Bullowa S, Negbi M (1975a) Germination characters in wild and cultivated *Anemone coronaria* L. Euphytica 24:213–220

Horovitz A, Galil J, Zohary D (1975b) Biological flora of Israel. 6 *Anemone coronaria* L. Isr J Bot 24:26–41

John E, Turkington R (1997) A 5-year study of the effects of nutrient availability and herbivory on two boreal forest herbs. J Ecol 85:419–430

Knight AP, Walter RG (2001) Plants affecting the digestive system. In: Knight AP, Walter RG (eds) A guide to plant poisoning of animals in North America. Teton New Media, New York, pp 80–141

Koniak G, Noy-Meir I, Perevolotsky A (2009) Estimating multiple benefits from vegetation in Mediterranean ecosystems. Biodivers Conserv 18:3483–3501. doi:10.1007/s10531-009-9656-9

Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol Evol 12:474–478

Lavorel S, McIntyre S, Grigulis K (1999) Plant response to disturbance in a Mediterranean grassland: how many functional groups? J Veg Sci 10:661–672

Mason C, MacDonald SM (2002) Responses of ground flora to coppice management in an English woodland–a study using permanent quadrates. Biodivers Conserv 11:1773–1789

McIntyre S, Lavorel S, Tremont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. J Ecol 83:31–44

Milchunas D, Noy-Meir I (2002) Grazing refuges, external avoidance of herbivory and plant diversity. Oikos 99:113–130

Mwendra EJ, Saleem MAM (1997) Infiltration, surface runoff and soil losses as influenced by grazing pressure in the Ethiopian highlands. Soil Use Manage 13:29–35

Naveh Z, Whittikar RH (1979) The conservation of ecological diversity of Mediterranean ecosystems through ecological management. In: Duffey E, Watt AS (eds) The scientific management of animal and plant communities for conservation. Blackwell, Oxford, pp 605–622

Ne'eman G (2003) To be or not to be—the effect of nature management on flowering of *Paeonia mascula* (L.) Miller in Israel. Biol Conserv 109:103–109

Noy-Meir I, Oron T (2001) Effects of grazing on geophytes in Mediterranean vegetation. J Veg Sci 12:749–760

Noy-Meir I, Gutman M, Kaplan D (1989) Responses of Mediterranean grassland plants to grazing and protection. J Ecol 77:290–310

Oz E, Dafni A (1991) The effect of forest opening on the flowering regime of *Lilium candidum* L. on the Carmel. In: Proceedings of the Carmel research conference II vol 6. Haifa and Galilee Research Institute, pp 29–34 (in Hebrew)

Perevolotsky A (2006) Integrating landscape ecology in the conservation of Mediterranean ecosystems: the Israeli experience. Isr J Plant Sci 53:203–213

Perevolotsky A, Seligman NG (1998) Role of grazing in Mediterranean rangeland ecosystems. Bioscience 48: 1007–1017

Perevolotsky A, Ettinger E, Schwartz-Tsachor R, Yonatan R (2003) Management of fuel breaks in the Israeli Mediterranean ecosystem: the case of Ramat Hanadiv Park. J Mediterr Ecol 3:13–22

Polley HW, Detling JK (1989) Defoliation, nitrogen, and competition: effects on plant growth and nitrogen nutrition. Ecology 70:721–727

Proffitt APB, Jarvis RJ, Bendottii S (1995) The impact of sheep trampling and stocking rate on the physical properties of a red duplex soil with two initially different structures. Aust J Agr Res 46:733–747

Raunkiaer C (1934) The life forms of plants and statistical plant geography. Clarendon Press, Oxford

Shmida A, Dafni A (1989) Blooming strategies, flower size and advertising in the "lily-group" geophytes in Israel. Herbetia 45:111–123

Stone EC (1951) The stimulative effect of fire on the flowering of the golden brodiaea (*Brodiaea ixiodes* Wats. Var. *lugens* Jeps.). Ecology 70:1286–1293

Tadmor NH, Brieghet A, Noy-Meir I, Benjamin RW, Eyal E (1975) An evaluation of the calibrated weight-estimate method for measuring production in annual vegetation. J Range Manage 28:65–69

Taylor KL, Grace J, Marx BD (1997) The effects of herbivory on neighbor interactions along a coastal marsh gradient. Am J Bot 84:709–715

Tilman D (1990) Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3–15

Todd SW, Hoffman MT (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecol 142:169–178

Tyler C, Borchert M (2002) Reproduction and growth of the chaparral geophyte, *Zigadenus fremontii* (Liliaceae), in relation to fire. Plant Ecol 165:11–20

van der Koppel J, Rietkerk M, Weissing FJ (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends Ecol Evol 12:352–356

van der Wal R, Egas M, van der Veen A, Bakker J (2000) Effects of resource competition and herbivory on plant performance along a natural productivity gradient. J Ecol 88:317–330

Wallach AD, Inbar M, Shanas U (2009) Roe deer and decapitated Anemone flowers. Isr J Plant Sci 57:103–106

Wardle DA, Barker GM (1997) Competition and herbivory in establishing grassland communities: implications for plant biomass, species diversity and soil microbial activity. Oikos 80:470–480

Williams PH, Haynes RJ (1995) Effect of sheep, deer and cattle dung on herbage production and soil nutrient content. Grass Forage Sci 50:263–271