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Long-term Trade-Offs Among Herbage Growth, Animal Production, and Supplementary Feeding in Heavily Grazed Mediterranean Grassland☆

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ABSTRACT

A 17-yr grazing trial was conducted in the eastern Galilee of Israel to quantify trade-offs among the responses of pasture and livestock productivity, duration of grazing, amount of supplementary feed, and profitability to higher stocking density during the growing season of a Mediterranean grassland. Treatments included two stocking densities and two grazing protocols. The stocking densities throughout the grazing period were 0.55 animal unit (AU)·ha^{-1}, which is common in this region, and 1.1 AU·ha^{-1}, which is considered high. The grazing protocols were continuous grazing throughout the grazing season and split-paddock grazing in which the herd grazed one subpaddock from the onset of grazing until the pasture was depleted, after which the herd was moved to the second ungrazed subpaddock. Under both protocols, heavier stocking density reduced standing biomass of the whole paddock at the end of the growing season by 43% and grazing duration during the subsequent dry season by 38% but increased the daily consumption of supplementary feed and the weaned live-weight production per unit area. Under continuous grazing the high stocking density of 1.1 AU·ha^{-1} was maintained throughout the grazing season for 17 consecutive yr with no detectable effect on productivity of the pasture, typical to the resilience of Mediterranean grasslands that have been grazed for thousands of years. The lower pasture biomass production was compensated by higher weaned calf production. At the current local prices, the heavier stocking density was close to the economically optimal stocking density for the pasture in the region. It is concluded that on Mediterranean grassland intensive use of the pasture with high stocking density during the growing season can be economically feasible in those cases where the feed requirement of the herd can be maintained throughout the growing season.

Introduction

Livestock stocking rates on Mediterranean rangelands are commonly determined by a combination of trial and error, accumulated experience, local practice, and largely intuitive professional recommendations. These methods served the producer well enough in the past, when stocking rates were sufficiently low that the nutritional needs of the livestock could be fully met by the range. But in modern economies, such stocking rates cannot support economically viable production systems (Holochek et al., 1998); stocking rates rise inevitably. As that happens, range management becomes more complex and there is a greater need for systematic study of key management decisions under controlled conditions (Lodge and Johnson, 2008).

As stocking rates rise, impacts of grazing on the pasture vegetation become more pronounced, supplementary feeding is required, costs increase, and all these responses defy easy prediction (Macleod and Mcintyre, 1997; Fynn and O'Conner, 2000). The constantly changing interannual and intra-annual availability and quality of the pasture vegetation, which determine both the nutritional intake of the grazing animals and the role of supplementary feeding, create trade-offs among the responses of the vegetation, the livestock, and the cost/benefit ratio of the grazing enterprise (Ratcliff, 1986; Rosiere, 1987; Holochek et al., 1998; Baron et al., 2002; Barry et al., 2005). Quantifying the trade-offs can contribute to more effective enterprise management (Savory and Butterfield, 1998).

In eastern Mediterranean grasslands dominated by annual species, the strongly seasonal pasture cycle is characterized by a mild, rainy winter-spring growing season and a hot, dry summer-autumn season (Seligman, 1996). Herbaceous plant production determines the carrying capacity of rangeland for livestock husbandry. But it is difficult to quantify it over large areas required to maintain viable herds, because it is influenced by climatic factors as: rainfall amount and distribution,

☆ NOTE: Botanical names according to Feinbrun-Dothan and Danin, 1991.

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temperature and humidity, the vegetative composition of the range and complex habitat characteristics that include topography, rock cover, soil depth and mineral availability (Seligman and Van Keulen, 1989; Burke et al., 1997; Leriche et al., 2001; Augustine, 2003).

Appropriate stocking rates under such conditions are dependent not only on productivity of the pasture vegetation and the supplementary feeding protocol, but also on the responses of vegetation and the livestock to grazing pressure, timing of grazing, and grazing protocol (Heitschmidt et al., 1987; Gutman et al., 1990). In general, the amount of standing biomass in the pasture decreases with increasing stocking rate (Hooper and Heady, 1970; Rosiere, 1987; Baron et al., 2002). Change in the standing biomass of a growing sward depends on the balance between the rate of pasture growth and the rate of forage consumption by the grazing herd. Heavy stocking at the beginning of the growing season can prevent the increase of standing biomass and fix the sward at a low equilibrium level far below that required for adequate animal nutrition (Noy-Meir, 1975). Deferment of heavy stocking at the beginning of the growing season can prevent the fall to a low stable equilibrium (Gutman et al., 1999). On the other hand, the production of the herd is dependent on the maximum use of the highly nutritious pasture forage during the short growing season.

Previous studies have shown that the Mediterranean pasture in the region can maintain a relatively high stocking rate without compromising the continued productivity of the range (Gutman et al., 1999; Sternberg et al., 2015). The first aim of the present study was to determine the maximum stocking rate that could be sustained throughout the growing season of Mediterranean grassland in a 500-mm-rainfall region without causing a long-term declining trend. The second aim was to quantify biological and economic trade-offs among pasture productivity, animal production, and supplementary feeding under different stocking regimens that test the limits of what is currently regarded as the feasible operating space.

Materials and Methods

Study Site

The experiment was conducted during 1994–2010 at the Karei Deshe Experimental Farm, located in eastern Galilee in northeastern Israel (35°35'E; 32°55'N; altitude 60–250 m a.s.l.). The topography is hilly, with slopes generally less than 20° (Seligman et al., 1989) covered with basaltic rock with an average cover of 30% (Gutman and Seligman, 1979). The soil is a fertile brown basaltic protogrumosol of variable depth but seldom deeper than 60 cm. The area has a Mediterranean climate, characterized by mild, wet winters with mean minimum and maximum temperatures of 7°C and 14°C, respectively, and hot, dry summers with mean minimum and maximum temperatures of 19°C and 32°C, respectively (Gutman and Seligman, 1979). The average annual rainfall between 1963 and 2010 was 557 mm. The seasonal rainfall (mostly in winter and spring between 1994 and 2010 at Karei Deshe Experimental Farm, with its wide variations among years and months, is shown in Fig. 1. The vegetation is a species-rich hemicryptophytic grassland (Zohary, 1973) dominated by *Hordeum bulbosum* L., *Echinops viscosus* DC., *Bituminaria bituminosa* L., and many annual species that constitute the bulk of the forage for beef herds (Sternberg et al., 2000).

Experimental Design

The study was based on two stocking densities and two grazing management protocols. The two stocking densities were moderate (M, 0.55 cows·ha^{-1}) and high (H, 1.1 cows·ha^{-1}) (Scarnecchia and Kothmann, 1982). On average, grazing began on 26 January, after deferment of grazing for an average of 70 days after the first rains to enable pasture establishment (Fig. 2). That left 76 days for grazing during an average growing season. The two grazing management protocols were continuous grazing during the grazing season (C) and a split-paddock

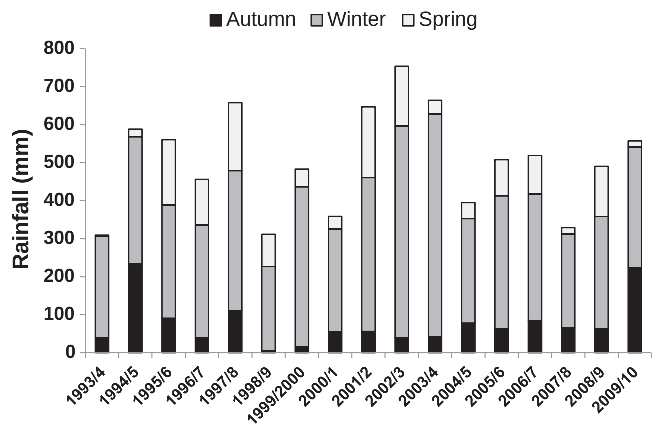

Fig. 1. Seasonal rainfall, 1994–2010, at Karei Deshe Experimental Farm. Autumn indicates September through November; Winter, December through February; Spring, March through May.

protocol (S) that represented the common practice of shifting herds between multiple paddocks on a ranch. Under protocol S each paddock was divided into two equal subpaddocks designated early (E) and late (L). Grazing began in subpaddock E at the end of deferment, at the same time it began in the C-treatment paddocks. Animals were moved to the second, hitherto ungrazed subpaddock (L) after the end of the growing season or earlier if the height of the standing biomass was reduced to an ocular estimate of less than 5 cm. When grazed, the stocking density was high—1.1 cows·ha^{-1}—in the grazed subpaddock of the moderate split-paddock grazing management protocol and very high—2.2 cows·ha^{-1}—in the heavy split-paddock treatment.

The two main-treatment stocking densities (M, H) and the grazing-management protocols (C, S) combined to form four main treatments: MC, MS, HC, and HS. In addition, the subpaddocks of the split-paddock grazing protocol gave rise to four secondary treatments: MS_E, MS_L, HS_E, and HS_L. The main treatments could be analyzed on a whole-paddock basis for biomass production, grazing duration, and animal performance. The secondary treatments could be analyzed only for stocking rate, biomass production, and grazing duration.

All treatments were replicated twice, and the areas of the eight main paddocks ranged from 21 ha to 35 ha. Movement of the herds in the split-paddock treatments was synchronized between replicates. Treatments

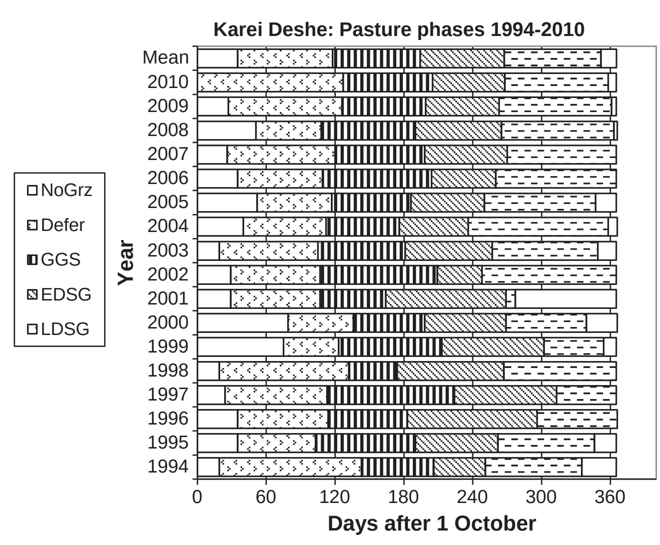

Fig. 2. Phases of the yearly pasture cycle at the experimental site during 1994–2010. NoGrz indicates no grazing in experimental paddocks; Defer, grazing deferment early in the growing season; GGS, green grazing season; EDSG, early dry season grazing; LDSG, late dry season grazing.

were maintained for 17 yr between 1994 and 2010 without change in order to capture the long-term responses of the vegetation under the wide yearly variations in climatic conditions and pasture productivity.

Livestock and Supplementary Feeding

The paddocks were stocked with animals drawn from the commercial beef suckler herd that had a concession to graze on the experimental farm. These were mature, medium-frame Simford (Simmental × Hereford) crossbred cows with about 20% blood from local eastern Mediterranean breeds. They had an average body weight of 432 ± 15 kg (≈1 AU) when the calves were weaned at the beginning of summer. At weaning, the cows and calves were weighed after overnight fasting and all calves were removed from the paddocks. Pregnancy was determined by rectal palpation in September to calculate the conception rate of the herd.

Between 1994 and 2002 new herds were reconstituted each year for logistics and management reasons imposed by the commercial herd owners. From 2003 onwards until 2010 arrangements were made to have the same herd graze each treatment every year. Replacements were made only to compensate for deaths or infertility. As a consequence, there were small deviations from the planned stocking density during the 17-yr duration of the experiment. Data on animal performance relate to the 2003–2010 period only when the same herds (except for replacements due to mortality or infertility) grazed the same paddocks every year.

No feed supplements were provided during the growing season and at the beginning of the dry season. Supplementary feeding (mainly poultry litter) was initiated at the end of the abundant dry pasture period. During the late dry period in the summer, the cattle were given unrestricted ad lib access to poultry litter as a source of nitrogen (N), to compensate for the protein deficiency of the dry forage (Holzer and Levy, 1976; Silanikove and Gutman, 1992). The amount of supplementary feed available to the herds was weighed and renewed whenever the previous amount was consumed so that the amount supplied to each paddock was the amount consumed by the herds. The composition of the poultry litter was 73% dry matter (DM), 24% ash, 23% crude protein (CP), 55% neutral detergent fiber (NDF), and metabolizable energy (ME) concentration of 1.6 Mcal·kg^{-1} (DM basis), which was similar to that of the dry pasture (1.6–1.7 Mcal·kg^{-1}). The higher CP and lower NDF compared with the dry pasture were among the factors that motivated the animals to ingest poultry litter (Landau et al., 2011). When the animals were not stocked in the grazing trial, they were allotted to other paddocks on the experimental ranch and given access to supplementary feed, as required for maintenance.

Vegetation Sampling and Analysis

The standing biomass in the paddocks was estimated by placing 25 × 25 cm quadrats at random along permanent transects that traversed all the experimental paddocks, and all above-ground standing herbaceous biomass in each quadrat was harvested. On each sampling date 20 samples, at least 10 m apart, were harvested in each of the 12 paddocks. The harvested plant material was oven-dried at 65°C and weighed. Henceforth all references to herbage biomass and consumption are on a DM basis. The biomass was sampled four times every year: 1) at the end of the early green pasture phase marking the transition between the grazing deferment period and the beginning of the green pasture season (January–February), 2) at the end of the green pasture phase marking the peak of vegetation growth (April) and before the range transitioned to the early dry season, 3) at the end of the early dry pasture phase marking the end of the abundant dry pasture period in early summer and before the transition to the late dry season and the beginning of supplementary feeding (June), and 4) at the end of the late dry pasture phase toward the end of summer marking the conclusion of the grazing season (August–September). The second and third sampling dates were determined by visual estimation of the phenology of the annual vegetation, and each sampling was conducted for all treatments within a few days. Note that the pasture phases relate to the state of the vegetation and not to grazing duration in the separate treatments.

Herbage Consumption

Above-ground production of an ungrazed pasture in any one season can be estimated by harvesting the herbage at the end of the growing season. An estimate of herbage production in a grazed paddock requires an estimate of herbage consumption by the herd during the growing season. Direct determination of forage consumed by a free-grazing herd is too complex to be implemented throughout the duration of a long-term grazing trial (Holzer et al., 1986). We therefore used the biomass consumption values established in earlier studies of energy expenditure and tritium dilution in free-grazing beef cows at the experimental site (Holzer et al., 1986, 1990; Aharoni et al., 2004, 2009). These studies yielded daily DM consumption values by 400–500 kg cows of 12 kg·AU^{-1}·d^{-1} during the growing season when forage was abundant and cows could graze to satiation. This is a commonly cited normative value for herbage consumption of 1 animal unit days (AUD) (Redmon et al., 1995; Poppi, 1996; SRM, 1998; NRC, 2000; Volesky, 2004; Smart et al., 2010). Forage intake as a function of herbaceous pasture biomass was estimated from a satiation function that assumes that at a low biomass value, intake would be reduced to zero because the foraging efficiency of the animal is determined by the limits imposed by mastication and anatomical features of the lips and teeth of the animal. A function that estimates the herbage intake of an AU as a function of available herbaceous biomass with higher and lower grazing efficiencies can be defined as follows (Noy-Meir, 1975):

$$c = c_{max}\left(1 - e^{-k[V-Vr]}\right) \quad 1$$

where,

c	daily forage intake (kg·AU^{-1}·d^{-1})
c_{max}	satiation forage intake (kg·AU^{-1}·d^{-1}) (12 kg·AU^{-1}·d^{-1})
k	foraging efficiency factor (dimensionless)
V	sward biomass (g·m^{-2})
V_r	sward biomass below which beef cows cannot forage (g·m^{-2})
V_s	minimum sward biomass for satiation consumption

The foraging efficiency factor, k, determines the slope of the consumption function between V_r and V_s. Measurements in the field indicated that V_r on the study site was between 10 and 20 g·m^{-2} (Cohen, 1990). For more efficient and less efficient foragers, k was assumed to be 10 g·m^{-2} and 20 g·m^{-2}, respectively. Consequently, the values for k were 0.022 and 0.016, respectively, when daily satiation forage consumption V_s = 12 kg·AU^{-1} and the minimum green herbage biomass for satiation consumption is 120 g·m^{-2}. These consumption functions indicate that when the biomass was between 80 and 100 g·m^{-2}, intake was reduced from satiation intake to 8–11 kg·AUD^{-1}, depending on the foraging efficiency of the animal.

Annual Forage Production and Animal Nutrition

Annual forage production of a grazed sward is subject to the influence of grazing and trampling on the vegetation during the growing season and is obviously not the same as undisturbed production (Noy-Meir, 1976). In the present study, herbage production under grazing was estimated as the sum of the standing biomass at the end of the growing season and the herbage that was ingested by the cattle during the growing season. The consumption rate during the growing season was estimated with the above forage intake function based on 12 kg·AU^{-1}·d^{-1} when the standing green biomass was sufficiently abundant to enable the cows to forage to satiation and 8–10 kg·AU^{-1}·d^{-1} under heavy grazing when the biomass was reduced to less than 100 g·m^{-2}.

In a separate study when the herd was feeding on abundant dry pasture in summer, satiation consumption, as determined by the herd's energy balance, was found to be 6–7 kg·AU^{-1}·d^{-1} (Aharoni et al., 2004), which was similar to results reported by Van Dyne and Meyer (1964) for dry annual pasture vegetation in California. When, later in the season, the cows had access to supplementary feed, dry-pasture biomass consumption was estimated by subtracting the weight of supplementary feed DM consumed per AU from the above normative value. The digestibility and the ME concentration of the supplementary feed was similar to that of the dry pasture (Aharoni et al., 2004).

In the early summer, a large part of the dry biomass that "disappeared" was composed of seeds and weathering of the dry pasture (Gutman, 1977). However, during the late summer, when dry herbaceous biomass started to become depleted, the difference between midsummer biomass and the end-of-season residual biomass represented the dry forage consumption by the herds during that interval. We calculated the relationship between the amount of supplementary feed consumed by each animal and the availability of dry pasture biomass for daily consumption by one AU as follows:

$$K = a/b$$

where,

K daily amount of dry pasture available for consumption by one AU (kg·AU^{-1}·d^{-1})
a midsummer biomass minus end-of-season biomass (kg·ha^{-1})
b stocking density (AUD·ha^{-1})

The relation between K and the supplementary feed that was consumed during the late dry summer phase is a measure of the trade-off between the intensity of dry pasture utilization and the consumption of supplementary feed by the herd.

Grazing Efficiency in Relation to Stocking Rate

In order to compare the relationship between the results of this experiment with others that have investigated the relationship between stocking rate and pasture productivity, we also calculated the grazing pressure index (GPI) (Scarnecchia and Kothmann, 1982), harvesting efficiency (HE), and grazing efficiency (GE) of the treatments during the growing season when the effect of grazing pressure on the pasture dynamics is most relevant. These indices were calculated according to Smart et al. (2010):

GPI = Stocking rate during the growing season/Primary Production of the pasture (AUD·Mg^{-1}).
HE = Herbage intake during the growing season/Primary Production of the pasture (%).
GE = Herbage intake during the growing season/(Primary Production – residual end-of-season herbage) (%).

Cost/Benefit Estimate of Stocking Density Options

In order to get a preliminary idea of the economic feasibility of high stocking we calculated the balance (B) between the income, from weaned live weight per hectare, and the cost of supplementary feed using local normative prices during 2012:

$$Bm = Lm\,Pw - (Wfm\,Pf + Wrm\,Pr)$$
$$Bh = Lh\,Pw - (Wfh\,Pf + Wrh\,Pr)$$

where,

m, h moderate and heavy grazing density (AUD·ha^{-1})
L weight of feed (kg·ha^{-1})
W production of weaned LW (kg·ha^{-1})
Pw, Pf, Pr price of weaned LW, supplementary feed, and full ration ($·kg^{-1})

While the herd was on the experimental pasture the supplementary feed was poultry litter. When not on pasture, from the end of one grazing season until the end of grazing deferment during the next growing season, the herd was maintained on a full ration of poultry litter and hay. The local normative prices in 2012 were 9.2 $·kg^{-1} for weaned live weight, 100 $·ton^{-1} for poultry litter, 250 $·ton^{-1} for hay, and 150 $·ton^{-1} for full ration (2/3 poultry litter, 1/3 hay).

Statistical Analysis

The multiyear data were analyzed using the repeated measures analysis of variance (ANOVA) model constructed in the JMP 10.0 software (SAS Institute Inc., Cary, NC) to estimate overall significance of seasonality and treatment effects on biomass production. Factors examined in the model were treatment, year, season, and block. For comparisons among the secondary treatments, the years were treated as independent nominal values and the standard deviations of the average biomass values over the years were given as an indication of the between-year variability. Additionally, a two-way ANOVA was used to analyze responses of pasture utilization, supplementary feed consumed, live weight, and conception rate of herds in the experimental treatments. The differences between treatments were subjected to post hoc examination with the Tukey-Kramer (honest significant difference) test. The long-term trends in the amount of biomass were analyzed as a function of years regarded as a continuous variable.

Results

Phases of the Annual Grazing Cycle

In the broadest terms, the pasture year of the Mediterranean zone divides into two seasons, green and dry, but for management of grazing a more detailed subdivision was required (Fig. 2). The average date of the first effective rains (>20 mm) in Karei Deshe during 1994–2010 was November 4. Within 14 d after the first effective rains, the germinated herbage biomass reached about 10 g·m^{-2} (Svoray et al., 2008). During the early part of the rainy season, November through December, the predominantly annual-herbaceous vegetation was too sparse to enable beef cattle to forage effectively and grazing was deferred until the herbaceous biomass increased to a level that allows the livestock to ingest increasing amounts of herbage (Defer in Fig. 2).

The second phase is the green grazing season (GGS in Fig. 2) during which consumption of pasture by the grazing animal increases with availability of biomass until there is enough for satiation consumption, after which satiation consumption is maintained and remains more or less constant. During this spring phase, February through April, there is a surge of growth that provides the abundant high-quality forage on which livestock production on the range is critically dependent. Peak biomass production, at the end of spring, is followed by the early dry season phase at the beginning of the summer (EDSG in Fig. 2) during which there are sharp reductions in both amount and quality of herbaceous vegetation, which are caused by seed dispersal and rapid desiccation (Henkin et al., 2011). This phase is characterized by relatively abundant dry pasture.

The last phase is the late dry season at the end of summer (LDSG in Fig. 2) during which there is a gradual decline in the amount and quality of dry herbaceous biomass, as grazing and weathering proceed during the hot, dry summer. This phase is characterized by relatively sparse, low-quality pasture that necessitates supplementary feeding to

Table 1
Analysis of standing biomass during the grazing season (1994–2010)

	Biomass harvest[1]			
	Begin	Max	Mid	End
Model R^2	0.67***	0.82***	0.89***	0.83***
Effect	F values of explainable variation[2]			
Year	13.1***	8.6***	25.1***	14.2***
Treatment	1.58 NS	17.7**	23.2**	12.3**
Replicate	11.5**	5.2 NS	9.8*	8.7*
Treatment	Standing biomass (mean and significance)[3]			
MC	79 [a]	284 [ab]	177 [a]	101 [ab]
HC	73 [a]	163 [bc]	88 [c]	54 [c]
MS_E	71 [a]	161 [bc]	105 [bc]	68 [bc]
MS_L	71 [a]	361 [a]	179 [a]	112 [a]
HS_E	70 [a]	132 [c]	93 [c]	59 [c]
HS_L	79 [a]	327 [a]	147 [ab]	101 [abc]

[1] Begin indicates onset of grazing; Max, peak season; Mid, midsummer; End, end of grazing season.
[2] ***indicates $p < 0.0001$; **, $p < 0.001$; *, $p < 0.05$; NS, not significant.
[3] Letters indicate significant differences by Tukey-Kramer (honest significant difference) test.

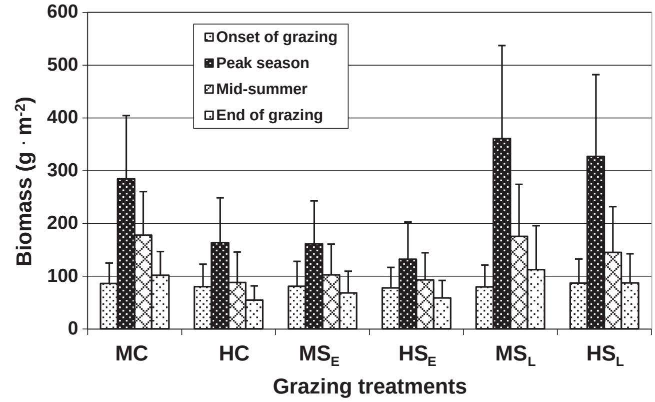

Fig. 3. Annual cycle of standing biomass in the moderate and heavy stocking rate treatments under continuous-grazing protocol and in the subpaddocks of the split-paddock-grazing protocol (Averages and standard deviations, 1994–2010). Main treatments: MC indicates moderate continuous; MS, moderate split; HC, heavy continuous; HS, heavy split. Subpaddocks: MS_E indicates heavy early; HS_E, very heavy early; MS_L, heavy late; HS_L, very heavy late.

maintain livestock production. The timing of the beginning and end of the pasture phases was determined by the amount of biomass and phenology of the vegetation. There was great variability in the length of the phases from year to year, with no year the same as the average duration of the phase.

The average duration of the growing season, from the initial greening of the vegetation until maturity and the onset of pasture desiccation, was 146 d. In all treatments, grazing was deferred for an average of 70 days after the first rains when the biomass of the herbaceous vegetation reached 76 ± 5.5 g·m^{-2} (Table 1) and the average height was 5 to 10 cm. On average, grazing began on 26 January, after deferment of grazing (Fig. 2). That left 76 days for grazing during an average growing season.

Grazing Duration

The grazing duration of the herds coincided with the pasture phases only in the continuous grazing treatments at the lower stocking density. The herds in the split-paddock treatments were moved from the MS_E and HS_E subpaddocks to the MS_L and HS_L subpaddocks, respectively, when the pasture vegetation was grazed down to a level below 3 to 5 cm. This took place on an average of 25 to 28 d before the peak of the growing season (end of "main green phase") in the case of HS_E and on an average of 16 d after the peak in the case of MS_E. In the summer, the herds remained in moderately grazed paddocks until October to November, depending on the occurrence of the first rain, but in the heavily grazed paddocks they had to be removed toward the end of August. Consequently, during the 17 yr of the experiment, the herds on average were on the pasture for almost 252 days of the year at the moderate stocking rate (146 AUD·ha^{-1}), and for 209 days at the heavy stocking rate (227 AUD·ha^{-1}). In all paddocks, except MS_L and HS_L, grazing started at the end of the grazing deferment period and ended at the beginning of autumn, when the pasture biomass was grazed down to between 54 and 112 g·m^{-2} (Fig. 3; Table 1).

Standing Biomass

When the herds started grazing, the long-term average standing green biomass in the paddocks was between 70 and 79 g·m^{-2}. Subsequently, the amount of standing biomass reflected the grazing density imposed on the different paddocks (Table 1; Fig. 3). The standing biomass in the HS_E paddocks was determined at the peak of the growing season and not when the herds were moved from the paddocks, as estimated biomass was less than 80 g·m^{-2}. Removing the herds before the peak season gave the pasture about 25 days of undisturbed growth during which the sward biomass increased to 132 g·m^{-2}. Initiation of grazing in the HS_L subpaddocks before the end of the growing season reduced the dry season standing biomass to below that measured in the MS_L subpaddocks into which the herds entered after the growing season ended. The standing biomass in the continuously grazed paddocks was inversely proportional to the stocking rates. At the end of the growing season, the biomass in the HC treatments was similar to that in the MS_E treatments, which is consistent with the fact that their stocking rates during the growing season were essentially the same (Fig. 3). There was no obvious long-term trend in the amount of peak biomass that could be related to the experimental treatments. The statistics for the relationship between biomass and year for three representative protocols—very high (HS_E) and moderate (MC) stocking densities and very low stocking density during the growing season (HS_L) —showed that almost all the trends were not significant and on the whole indicated a weak negative trend. This is possibly related to the fact that the average rainfall in the first 11 years of the experiment was 523 mm, but only 449 mm during the last 6 years. The only protocol that exhibited a positive (not significant) trend was the one with the highest stocking density during the growing season (HS_E).

Distribution of Explainable Sum of Squares

The interannual variation of the standing biomass was large (Fig. 3), evidently because of the large interannual variation in rainfall amount (between 310 and 754 mm) and distribution. Correlation between annual rainfall and the biomass determinations on all harvest dates was low (r = 0.25–0.50). The allocation of explained variance to the various effects varied widely between harvests ($R^2 = 0.67$ to $R^2 = 0.89$): "Year" accounted for 36–84%, "Grazing treatment" for 4–54%, and "Replicates" for 3–6%. All these effects were highly significant (Table 1). When the herds were introduced into the paddocks at the onset of grazing, there were small differences in the standing biomass among the treatments, but they spanned a narrow range of 13 g·m^{-2}. The differences among treatments were greatest at the end of the growing season and were largely maintained throughout the summer until the end of the grazing season (Table 1; Fig. 3).

Grazing Efficiency in Relation to Grazing Pressure

The stocking densities were equivalent to growing season stocking rates of 41 to 43 AUD·ha^{-1} at the moderate density and 73 to 85 AUD·ha^{-1} at the high density (Table 2; Fig. 2). If we add the period of grazing during the dry season, the duration of which depended on the

Table 2
Derivation of the estimate of grazing pressure index, harvesting efficiency, and grazing efficiency during the growing season, 1994–2010

	Main grazing treatments				Subpaddocks			
	MC	MS	HC	HS	MS_E	MS_L	HS_E	HS_L
SR: Stocking rate during growing season only (AUD·ha^{-1})[1]	43	41	85	73	105	0	97	59
DHI: Daily herbage intake during growing season (kg·AU^{-1}·d^{-1})[2]	12	11	11	10	11	0	9	12
I: Growing season herbage intake (Mg·ha^{-1}) [I = SR·DHI/10^3]	0.519	0.451	0.930	0.725	1.151	0	0.875	0.703
PSC: Peak standing biomass (Mg·ha^{-1})	2.845	2.609	1.635	2.295	1.612	3.607	1.319	3.271
PP: AHP (Mg·ha^{-1}) [PP = PSC + I]	3.364	3.060	2.565	3.020	2.763	3.607	2.194	3.974
R: Residual end-of-grazing biomass (Mg·ha^{-1})	1.030	0.940	0.550	0.710	0.720	1.160	0.580	0.840
GPI: Grazing pressure index (AUD·Mg^{-1}) [GPI = SR/PP]	12.8	13.4	33.1	24.2	38.0	0.0	44.2	14.8
HE: Harvest efficiency (%) [HE = I/PP]	15.4	14.7	36.3	24.0	41.7	0.0	39.9	17.7
GE: Grazing efficiency (%) [GE = I/(PP-R)]	22.2	21.3	46.2	31.4	56.3	0.0	54.2	22.4

AHP indicates annual herbage production; AU, animal units; AUD, animal unit days; SR, stocking rate.
[1] Grazing days per ha during the growing season.
[2] Daily herbage intake of green forage per AU according to Fig. 1.

stocking density, the lower and higher stocking rates amounted to 120 to 146 and 186 to 227 AUD·ha^{-1}, respectively.

Expressing grazing pressure during the growing season in terms of the GPI yielded values between 13 and 44 AUD·Mg^{-1} (Table 2), which are similar to those reported by Smart et al. (2010), despite the large differences in vegetation and seasonality between the rangelands of the North American Great Plains and the Mediterranean grasslands. Both grazing efficiency and harvest efficiency were linearly related to GPI (Fig. 4) as in the Smart et al. (2010) data. Their range of the efficiency values was higher than in our case, possibly because instead of dividing by peak standing herbage biomass, we divided by total estimated herbage production (expressed as annual herbage production in Table 2).

Performance of the Herd and Supplementary Feeding

During 2003–2010, the live weights of cows and their conception rates were higher in the split-grazing than continuous-grazing treatments, but the differences were relatively small, so stocking rate had an overwhelming (almost proportional) effect on weaned live weight per unit area of pasture: The weaned calf production rates at the high and moderate stocking rates were 87–89 kg·ha^{-1} and 41–46 kg·ha^{-1}, respectively (Table 3). The replacement rate of the cows was irregular among treatments but highest under HC, the high stocking density grazed continuously (Table 3).

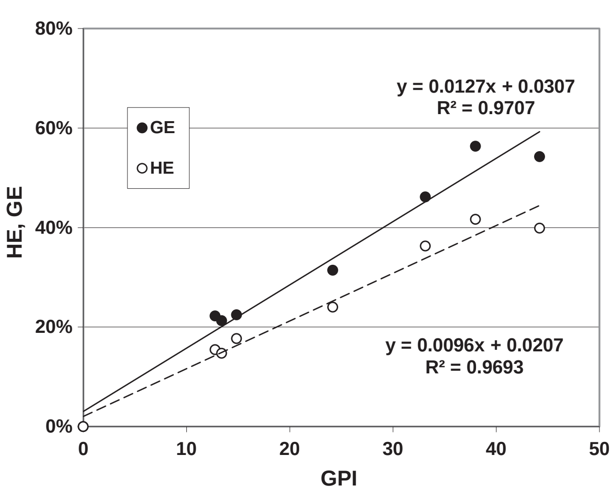

Fig. 4. The relation between the grazing pressure index (GPI, AUD·Mg^{-1}) and harvest efficiency (HE; herd forage intake/annual forage productivity) and grazing efficiency (GE; [herd forage intake–end-of-grazing residual herbage]/annual forage productivity).

The experimental herds were given ad lib access to poultry litter as a supplementary feed (Holzer and Levy, 1976). The amount that was consumed was clearly related to stocking density and to dry herbage availability during the late summer: As the availability of dry pasture biomass fell from 13.5–6.4 kg·AUD^{-1}, the consumption of supplementary feed rose from 4.5–7.3 kg DM. Even though the animals in the heavy-stocking-rate treatment were on pasture for a shorter period than those in the moderate stocking rate, their average daily consumption of supplementary feed per head was 64% higher (Table 3). During the early dry pasture phase, the fall in the amount of standing biomass was mainly due to seed dispersal and was much greater than the potential intake of dry pasture by the grazing animals. The dry pasture became limiting only during the late dry pasture phase and necessitated supplementary feeding that increased sharply as the available dry pasture dropped below 13.5 kg·AU^{-1}·d^{-1}. When the herd is not given supplementary feed, increase in stocking rate commonly reduces animal performance (Hart et al., 1997; Manley et al., 1997).

Cost/Benefit Estimate of Stocking Density Options

Despite the higher cost of feeding the herd both on and off the range at the heavier stocking, the cost of the additional feed was much less than the extra value of the higher weaning weight per unit area. Consequently, despite the shorter period on the dry summer range and the more intensive use of the dry pasture the higher stocking rate was more profitable at the current local prices of weaned calf live-weight and supplementary feed (Table 4).

Discussion

Year-to-Year Variation in Herbaceous Biomass Production

The wide year-to-year variation in standing biomass, as revealed by the standard deviations of all the experimental treatments (Fig. 3), is a result of the complex interactions among the year-to-year variations in climatic conditions (Fig. 1), the dynamics of nutrient availability in the soil (Zaady, 2005), and the botanical composition of the vegetation (Sternberg et al., 2015). The "year effect" accounted for a greater proportion of the variation in the data than the treatments (Table 1). The correlation between annual biomass production and annual rainfall amount or distribution at the experimental site was found to be moderate (Golodets et al., 2013). An attempt to establish a multivariate correlation between the standing crop of an annual species rangeland and more than 20 climatic variables, including day-degrees, evaporation, and longest dry period, met with moderate success (George et al., 1989). However, despite the climatic "noise" that accompanied

Table 3
Pasture utilization, supplementary feed consumed, live weight, and conception rate of herds is the experimental treatments, 2003–2010 (average and standard deviation)

Treatment	MC	MS	HC	HS	Yr	Treatment	Yr × Treat.
No. of cows in paddock	16 ± 1	15 ± 2	27 ± 4	29 ± 4			
Days in treatment paddocks	279 ± 19	277 ± 18	198 ± 26	205 ± 27			
Days out of treatment paddocks	86	88	167	160			
Stocking rate, growing + dry seasons (AUD·ha^{-1})	156 ± 10	168 ± 29	223 ± 28	233 ± 60			
Residual end of grazing season biomass (g·m^{-2})	103	94	55	71			
Daily supplementary feed consumption (kg·AU^{-1}·d^{-1})	4.2 ± 2.2^{a}	4.6 ± 2.5^{a}	7.9 ± 2.5^{c}	6.2 ± 2.2^{b}	< **.0001**	< **.0001**	< **.0001**
Duration of supplementary feeding (days)	131 ± 36	134 ± 35	76 ± 36	76 ± 37			
Seasonal supplementary feed consumption (kg·AU^{-1}) (kg·A^{111}·season^{-1})*	571 ± 325^{ab}	600 ± 331^{a}	620 ± 347^{a}	478 ± 302^{b}	< **.0001**	**0.0107**	< **.0001**
Cow live weight on entry (kg)	407 ± 30^{b}	434 ± 25^{a}	404 ± 19^{b}	412 ± 28^{b}	< **.0001**	**0.001**	0.941
Conception rate (%)	73 ± 13^{a}	76 ± 13^{a}	70 ± 6^{a}	78 ± 5^{a}	0.542	0.502	0.0505
Weaned calf weight (kg·calf^{-1})	127 ± 27^{a}	130 ± 23^{a}	124 ± 20^{a}	126 ± 23^{a}	< **.0001**	0.840	0.962
Weaned calf production (kg·ha^{-1})	46 ± 12^{a}	41 ± 7^{a}	89 ± 17^{b}	87 ± 17^{b}	**0.0012**	< **.0001**	0.277

Bold show significant values.
Different letters show statistically significant differences between treatments.

the present study, the larger between-treatment differences in standing biomass were significant in both the growing and dry seasons (Table 1).

Herbage Dynamics at Different Stages of the Grazing Cycle

Under the continuous grazing management protocol (C) the herd could be maintained on pasture from the end of deferment until the end of the growing season at both the moderate (M) and high (H) stocking densities, although there was less standing biomass under the heavier grazing both at the peak of the growing season and at the end of the dry season (Fig. 3). In the split paddock (S) grazing-management protocol, the stocking density during the growing season was 1.1 AU·ha^{-1} in the MS_E subpaddocks and 2.2 AU·ha^{-1} in the HS_E subpaddocks. The herds in the HS_E subpaddocks had to be evacuated before the end of the growing season, so we conclude that on grasslands like those of the study site, grazing cannot be sustained throughout the growing season at a stocking density of 2.2 AU·ha^{-1}.

The length of the grazing season and the need for alternative supplementary feed sources is part of the evaluation of the treatments for management decisions (Hooper and Heady, 1970). During the 2003–2010 period, when the same herd grazed each paddock every year, the dry summer pasture maintained the herds at the heavy stocking densities of treatments HC and HS for a shorter time than it did for the medium stocking densities of treatments MC and MS, and the pasture was used more intensively, leaving less residual vegetation at the end of the grazing season (Table 3). The amount of supplementary feed that was consumed during the duration of grazing in the experimental paddocks does not include the feed requirements of the herds when they were out of the paddocks between the end of the summer grazing season and the end of the deferment period in the subsequent year (Table 3).

On Californian annual rangeland the optimal amount of residual DM at the end of the grazing season was found to be about 90 g·m^{-2} (Hooper and Heady, 1970), which is within the range of the present moderate-grazing treatments but above that of our heavy-stocking treatments (Table 3). Nevertheless, the lower residual DM in the heavy-grazing treatments did not affect the recovery of the pasture vegetation. It appears that there was no mulch effect of the dry vegetation litter and that the viability of the seeds produced and dispersed early in the dry season was unrelated to the end-of-season residual biomass. Consequently, the differences between stocking-rate treatments in standing biomass at the onset of the grazing season were small (Table 1) and no long-term decline in biomass at the onset of the grazing season was detected.

The relationship between grazing pressure and the seed bank is complex and involves the effects of grazing on the botanical composition of the seed yield and the seed bank (Sternberg et al., 2003). After seed production and dispersal, seed survival dynamics during the summer, under heavy granivory by ants, small animals, and birds, is another factor that determines the amount and composition of the residual seed store (Janzen, 1971; Hobbs, 1985; Samson et al., 1992). The overall effect of these factors in the present study suggest that the residual seed stocks left in the soil were enough to enable similar regeneration of the pasture vegetation in the subsequent growing season in all the treatments of the experiment despite considerable differences in residual end of season biomass.

Animal Performance

The live-weight of the cows and the conception rates were higher under the split-paddock protocol than under continuous grazing (Table 3), but these differences were relatively small compared with the differences in stocking rates and with other studies (Ratcliff, 1986; Gutman et al., 1990). The relative similarity in animal performance between treatments can be ascribed to the ad lib access of the herds to supplementary feed in summer, when the dry pasture was insufficient to maintain their performance. As a result weaned live-weight production in the heavy-stocking-rate treatments was almost double that under medium stocking rates, albeit at a higher cost in supplementary feed (Table 3). Similar results were reported elsewhere (Willms et al., 1986; Lodge and Johnson, 2008). Continuous heavy grazing that has often been accompanied by severe range deterioration (e.g., Willms et al., 1985; Hart and Ashby, 1998) had no detectable negative effects on the pasture vegetation on the study site. The practical implications of the trade-offs that were observed in the present trial depend on a combination of the herd owner's aims and the economic context of the grazing operation. This includes livestock prices, the cost of supplementary feed, and the fixed and variable costs attached to rangeland ownership and management. The resilience of the pasture vegetation under heavy grazing enables a greater fraction of the pasture to be used at the height of its nutritive value. As a first estimate of the economic feasibility of heavier stocking rates, we can compare the value of the extra weaned live weight under heavy grazing with the cost of extra feed. Under local economic conditions, with weaned beef-calf live weight at 9–10 \$·kg^{-1} and supplementary feed at 25–40 \$·ton^{-1}, the extra kg of

Table 4
Cost/Benefit estimate of stocking density options

Price of weaned live weight *(Pw)*	9.2	$ per kg
Price of supplementary feed *(Pf)*	100	$ per ton
Price of complete ration *(Pr)*	150	$ per ton
Grazing pressure	Moderate	High
Stocking density AU·ha^{-1}	0.58	1.1
Stocking rate AUD·ha^{-1}	162	228
Weaned LW kg·ha^{-1} *(L)*	40	89
Supplementary feed ton·ha^{-1} *(Wf)*	0.572	0.619
Complete ration ton·ha^{-1} *(Wr)*	0.686	2.086
Cost of feed $·ha^{-1} *(C)*	160	375
Value of weaned LW $·ha^{-1} *(V)*	368	819
Balance $·ha^{-1} *(B)*	208	444

AU indicates animal unit; AUD, animal unit days; LW, live weight.

weaned live weight per cow is worth 402 $\$\cdot ha^{-1}$ and the extra feed based on poultry litter and straw costs around 199 $\$\cdot ha^{-1}$. This is a promising margin of profitability, but a realistic estimate of economic advantage would have to consider additional costs incurred by the higher stocking density like a higher cow replacement rate (Table 3). Higher productivity following more intensive use of the green pasture was also demonstrated by Owensby and Auen (2013).

Cost/Benefit Estimate of Stocking Density Options

The higher profitability of heavier grazing is a reflection of the more intensive utilization of the highly nutritious green pasture during the growing season at the cost of foregoing a few weeks of grazing on the low-quality dry pasture in summer. Under continuous grazing, the herd could graze throughout the growing season at the higher stocking density and still leave enough green plant material to allow regeneration of the pasture in the subsequent growing season, at least for a period of 17 yr. If the grazing cannot be maintained to enable satiation intake for the whole of the growing season (as in HS_E subpaddocks), then the biological limit to higher stocking densities is exceeded, animal performance will be lower, and the economic balance would change. At the biological limit, satiation intake is at least 130 $g\cdot m^{-2}$ (Table 1, Fig. 3), enough to allow for seed production for pasture establishment in the subsequent year. Therefore in the present study, the limiting biological stocking density would be less than 2.2 $AU\cdot ha^{-1}$ and not much higher than 1.1 $AU\cdot ha^{-1}$. The ability of the pasture vegetation to regenerate after intensive use is characteristic of the herbaceous Mediterranean range in which annual species with efficient seeding strategies have evolved under centuries of intensive grazing (Sternberg et al., 2003, 2015).

Management Implications

We conclude that when grazing on Mediterranean-type annual grassland is deferred until the germinating pasture vegetation is well established, high stocking densities under continuous grazing that do not exceed 1.1 $AU\cdot ha^{-1}$ during the growing season can increase weaned live weight per unit area with no discernible long-term damage to the pasture. Such resilience is characteristic of Mediterranean grasslands that have been grazed intensively for thousands of years. Other grasslands that have been grazed also exhibit similar resilience (Milchunas and Lauenroth, 1995; Ruppert et al., 2014). The relationship between grazing pressure and grazing efficiency that measures the degree of utilization of the pasture biomass (Fig. 4) was surprisingly similar to the relationship in the Great Plains of North America (Smart et al., 2010), despite the large differences in vegetation, seasonality, and ecosystem characteristics.

When pasture is the mainstay of the herd and must supply feed for as long as possible during the year, the shorter grazing duration at the higher stocking densities exact a cost in additional supplementary feed. The trade-offs among greater animal production, the consequently shorter grazing season, and the heavier cost of supplementary feeding all depend on the grazing density under the specific conditions of each range. What emerges from the present study is that animal production depends largely on the intensity of the utilization of the highly nutritious pasture during the growing season. There is a trade-off between heavy use of the green biomass and the resultant shorter grazing duration during the subsequent dormant phase; these consequences of the trade-off are neutralized by the presence of greater quantities of supplementary feed and by profitability changes of a negative trade-off to a positive one. Nevertheless, there is a limit imposed by the need to maintain adequate nutrition of the herd throughout the growing season without compromising the regeneration of the pasture in subsequent years.

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