The effect of grazing and management measures on the vegetation of a dehesa – an agro-ecosystem formed during centuries by agro-sylvopastoral exploitation

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Azinheira: a fronteira que nos separa do deserto

(Der Steineichenwald ist die Grenze, welche uns, die Länder des Mediterranen Klimas, von der Wüste trennt).

von dem Portugiesen

Fernanda Dos Santos Amaro (1988)

Content

1 General introduction

1.1 Traditional cultural landscapes – the sylvo-agropastoral system "dehesa"

According to Montoya Oliver (1989), the dehesa is one of the characteristic ecosystems of the Iberian Peninsula, with the evergreen oak trees scattered in open savannah-like grassland as an outstanding, distinctive physiognomy. It is an example for an old cultural landscape developed through silvo-agropastoral use of the Mediterranean hard leave forest (Hampe, 1993). Silvo-agropastoral use is characterized through the combination of forestry use (firewood as well as cork production), cultivation and pasturing done mostly with mixed herds of cattle, pigs, goats, sheep and horses. Dehesa grassland, being listed in the Flora-Fauna-Habitat-Directive (Díaz et al., 2003), includes some of the most species-rich communities outside the tropics (Marañon, 1986, 1991). The high diversity both in flora and fauna depend mainly on the exploitation system of the dehesa (Lavado Contador et al., 2000; Díaz et al., 2003).

In this climatic zone, the Mediterranean hard leaves forest, the Bosque mediterráneo (Rivas-Goday & Rivas-Martínez, 1963), once covered huge areas of Mediterranean Spain and Portugal, and is now reduced to only small, for human hardly accessible areas. The original forest has been transformed during centuries into a pseudo-savanna with a density of holm oak of about 40 to 100 trees per hectare depending on tree age (Bernaldez, 1991). Besides the tree layer, which is mainly consisting of different oak-species (*Quercus ilex*, holm oak; *Q. suber*, cork oak; *Q. rotundifolia; Q. faginea*), this type of forest is composed of a shrub layer, which is very rich in species. The herbaceous layer was mainly composed of annual species such as *Agrostis castellana*, *Brachypodium distachyon*, *Leontodon longirrostris*, *Tuberaria guttata* and *Trifolium spp*. with more than 20 species / 400 cm^2 (Peco et al., 2003). To present the extensive livestock farming plays a crucial role in the Spanish dehesa (Schnabel, 1996; Montero et al., 1998). Related to this, local breeds of livestock have been developed, which have adapted best to the climatic conditions in the Mediterranean dehesas. Among this is the Iberian pig, the Merino sheep and the Berrenda and Retinta cattle (Montero et al., 1998). The origin of the dehesa is believed to lie as far in the past as the middle age, since the first references mentioning the Spanish dehesa goes more than a thousand years back (Montero et al., 1998).

Nowadays, about 3–3.5 Mio.ha is maintained in Spain from the formerly huge areas of dehesas. Out of these, about 632000 ha are still in agricultural use (Montero et al., 1998). Today, the dehesa is mainly found on oligotrophic soils in Mediterranean Spain. On eutrophic soils, most dehesas have been replaced by arable farming. Dehesas outside the area of Mediterranean Spain usually differ extremely in structure, function and management from the typical Mediterranean ones. Therefore, most dehesas are situated in the west and southwest of the Iberian Peninsula (Montero et al., 1998). With the Mediterranean climate and the low fertility of the soil, the dehesa has arisen as the only possible form of productive land use (Montero et al., 1998). Eventually, more important than the physical environment is the traditionally complex and variable use of a dehesa. On the shallower soils and the steeper slopes grazing usually predominates with mixed herds of cattle, sheep, goats and pigs. The better, deeper soils are cultivated periodically in cycles of four to five years. With grazing, cutting or controlled burning the shrub encroachment is counteracted (Figueroa & Davy, 1991). The most common adaptation to the climatic conditions is therophytism, with germination in autumn and flowering, fruiting and seeding until the end of spring or early summer. With outlasting in seed form throughout summer, the cycle starts again in autumn (Blanco Castro, 1997; Montero et al., 1998). The implication of a non-productive summer period has let to the system of transhumance, connecting the winter-pastures of the dehesa with the summer-pastures in the mountains in northern Spain (Blanco Castro, 1997). Transhumance signifies peregrination of herdsmen with herds between different pastures due to absence of all-season and sufficient fodder neither in summer nor in winter place (Lüdeke, 2005). However, with increasing labor costs, forage is nowadays rather brought to the livestock than livestock to forage.

The term dehesa describes both treeless and tree-covered pastures in Spain. However, as tree cover plays a decisive role in the development and use of a dehesa system, the present study deals only with tree-covered dehesas. In the south, southwest and west of the Peninsula, in areas with mild winters, a remarkable amount of acorns are produced by the oaks. Therefore, the most common type in these areas is a forest with large oak trees, which underlines in these regions the importance of acorn mast of the Iberian pigs compared to browsing (Montero et al., 1998). The trees are an essential component in the system of a dehesa (Montero et al., 1998), strongly influencing their neighbouring vegetation (Marañon, 1986). The tree cover effects stability and productivity of the dehesa grassland, and changes water balance, solar radiation, wind velocity, etc.

As most of the old, cultural landscapes, the Spanish dehesas are threatened through abandonment as well as intensification of farming. The decline of semi-natural grasslands can be observed throughout Europe (Losvik, 1988; Fischer & Stöcklin, 1997; Kahmen & Poschlod, 2004) and is especially causing a degradation of habitats in arid and semi-arid areas (Hammouda et al., 2003). Not only abandonment, but also agricultural intensification led within the last few decades to a considerable floristic change and a decrease in semi-natural ecosystems in Europe (Arianoutsou, 2001). With this decline, species restricted to these habitats are threatened due to a lack of habitat (Fischer & Stöcklin, 1997; Berlin et al., 2000). Furthermore, the substitution of traditional land use results in a loss of pastoral value, soil erosion, fire risk, a decrease in biodiversity, and a threat of vulnerable species (Bernaldez, 1991).

Abandonment of use in the Mediterranean dehesa results in growth of coarse vegetation and shrub encroachment. This leads to a loss of pastoral value, increase in fire risk and a decrease in biodiversity (Bernaldez, 1991). The intensification of use causes a desertification of the areas. With increasing grazing pressure, natural tree rejuvenation is restrained, and the herbaceous and shrubby layers become degraded. This implies increasing soil erosion and thus soil degradation not only in winter during heavy rainfalls, but also in dry summer due to wind. Instead of species rich grasslands, a cleared out landscape with steppes and desert develops (e.g. Arianoutsou, 1985, for Lesvos Island, Greece). With increasing decline in earnings, the risk of abandonment of the farms rises through mismanagement. The mostly poor rural regions lose with their environment even more parts of their often only resources, from which they managed to live for centuries through an adapted exploitation (Lavado Contador et al., 2000).

A special role in the pasturing of a dehesa plays the Iberian pig. In order to fatten the pigs with the fallen acorns, they been led since centuries into the oak forests. Beneath their grazing activities, pigs have special impact on vegetation due to their digging in the soil. With the disruption of normally dense vegetation cover, vegetation dynamics and patchiness increases, which mostly lead to an increase in plant diversity (Fensham et al., 1994; Micklich et al., 1996; Treiber, 1997; Beinlich, 1998). Both species from actual vegetation as well as from soil seed bank get opportunities for germination (Micklich et al, 1996; Beinlich, 1998; Poschlod & Ittel, 2005). Through digging, new niches and different successional stages are created, providing a mosaic of micro – sites, increasing not only species diversity, but, above all, facilitating competitively low species. This leads to a high temporal dynamic and spatial heterogeneity not only on the vegetation and community level (Poschlod, 2003), but also on the species level (Poschlod, 2005).

Most of the common, late-successional species in a dehesa (e.g. *Cistus* spec., *Lavandula* spec., *Genista* spec.) possess physical or chemical defences against grazing. Thus, grazing is often not sufficient in order to prevent shrub encroachment in these open grasslands. As a consequence, periodic ploughing (Sánchez et al., 2001) is traditionally used in the Mediterranean dehesa in order to control unwanted shrub vegetation. Due to the immense effort of ploughing in former times with animal driven ploughs, only small parts of a farm were ploughed at once. Nowadays, with the development of agricultural machinery, the dimension of the area ploughed in one procedure increased dramatically, standardizing big areas of a farm in their successional stage. In an extreme climate like the Mediterranean with high temperatures in summer and often heavy rainfall in winter, wind erosion in summer and rain erosion in winter are two of the endangerments accompanying ploughing (Hammouda et al., 2003). Furthermore, due to the bare soil left after ploughing, germination conditions, intensified by the endangerment of soil sealing, may be unfavourable. This makes ploughed fields often unfavourable for the development of new vegetation. Additionally, natural as well as by human started fires have been shaping Mediterranean landscapes decisively over centuries (Trabaud 1994, 2002). Many species have evolved strategies in order to survive periodic fires (Naveh, 1975; Pausas, 1999a). Due to human impact, the frequency of fire recently increased in the Mediterranean Basin and is expected to further increase as a result of global climate change in all Mediterranean type ecosystems (Beer & Williams, 1995; Pausas, 1999b, Pausas et al., 2004; Pausas, 2004). Land abandonment and climate change will not only change fire frequencies, but also fire intensities due to changing fuel accumulation, increasing temperatures and decreasing humidity caused by decreasing rainfall in the Mediterranean Basin (Pausas, 1999a, 2004). According to Pérez & Moreno (1998), more than 200,000 ha, of which 41 % were woods, have been burned annually in Spain over the last few decades.

1.2 Thesis outline

In the present thesis, a habitat-specific study about the system dehesa was accomplished. Since so far, only cattle grazing had been analysed in previous studies. Therefore, in my thesis I studied the effect of pig grazing and compared these management treatments to the traditional grazing regimes with mixed herds of cattle and pigs. Additionally, I studied the effects of other traditional managements, namely burning and ploughing, on the vegetation. Since vegetation composition may not only depend on management but also on the dispersal of seeds through the management treatments, studies on the endozoochorous seed dispersal by both cattle and pigs were included. Several management treatments included soil disturbance like rooting pigs or ploughing. Therefore, the soil seed bank from the differently managed areas was characterized, too. In addition, as an important factor for Mediterranean dehesa vegetation, the influence of fire on germination ecology was analysed. The aim of the study was therefore, not only to understand the effect of the management treatments on the vegetation but also the mechanism causing differences in the vegetation after the application of the management treatments.

Regarding this, Fig. 1.1 gives an overview about the topics being addressed in the individual chapters.

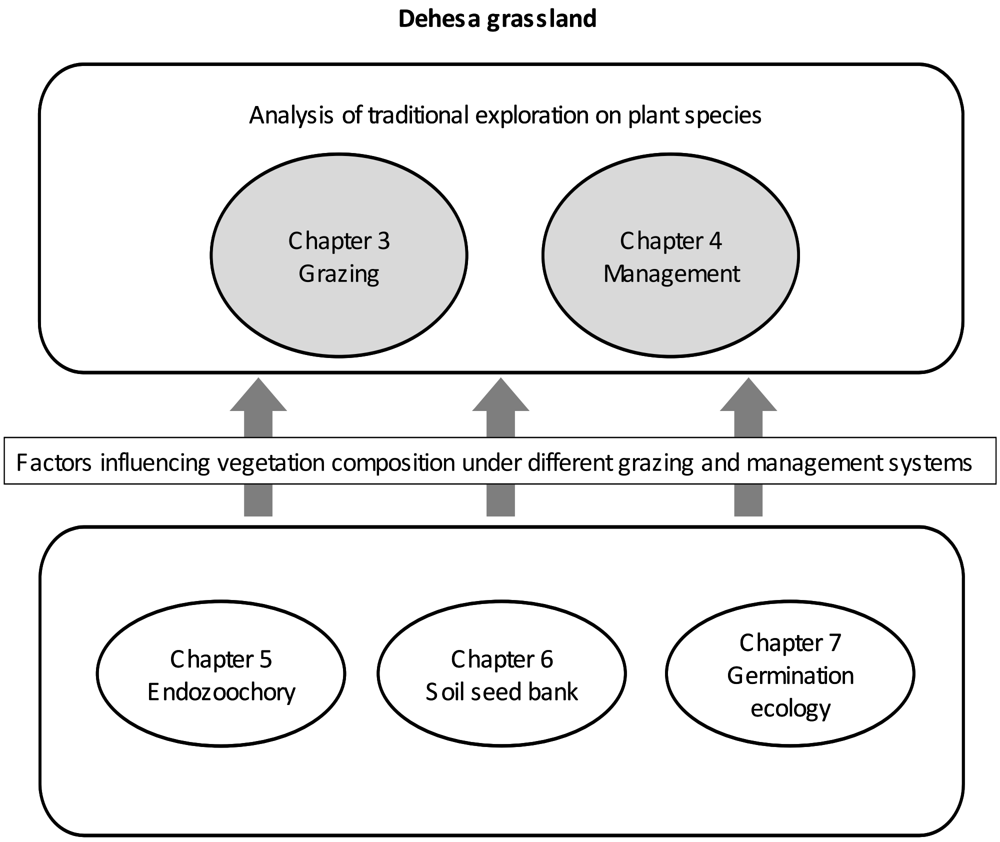

Fig. 1.1: Structure of the thesis with the chapters describing the effect of management and its influence on species adaptation.

Chapter 1 in the present work gives a general introduction together with a short outline of the subjects of the respective chapters. Information about the ecosystem dehesa, its development, actual situation and threats are given. In chapter 2, the study area and study site are described.

Chapter 3 focuses on the effect of changes in the traditional grazing system on vegetation. Therewith, different grazing regimes (cattle & pig grazing, pig grazing and fallow), which represent a disturbance gradient both regarding aboveground biomass and soil, are studied regarding species number and composition. Furthermore, in order to meet the requirements of the heterogeneous landscape, lower and upper slopes were analysed separately. In chapter 4, traditional managements, namely ploughing, burning and a combination of both, are analysed and compared with permanently grazed pastures without further treatments. Here, the question how single managements, which imply severe disturbances both to aboveground vegetation as well as to soil, affect vegetation development adapted to permanent grazing is addressed. Based on the question if different managements as well as slope zone influence the affect of drought on species composition, an analysis of soil moisture of the differently used areas is additionally incorporated. Furthermore, the influence of the different managements on shrub encroachment is also studied in chapter 4. In chapter 5 and chapter 6, dispersal capacity in space and time is analysed. Whereas chapter 5 deals with endozoochorous seed dispersal, chapter 6 addresses dispersal over time in terms of soil seed bank persistence. Dispersal of seeds by two common livestock in a dehesa, pigs and cattle, are compared in chapter 5. Another question is if species spectra of the endozoochorously dispersed species differ between the omnivorous pig and the herbivore cattle. Chapter 6 analyses the soil seed bank and compares it to the actual vegetation. In chapter 7, the influence of fire on germination of typical species of a Mediterranean type dehesa is analyzed based on a germination experiment simulating fire. Both heat and smoke treatments were applied to 27 species typical for the study site, a Mediterranean dehesa.

Finally, in chapter 8**,** conclusions are made with considerations about future requirements for conservation of cultural landscapes. It is advocated for a more holistic concept incorporating structure and diversity on landscape level in order to ensure the functioning of the landscapes. Creative alternatives for the traditional land use, stronger related to the particular situation and historical background of the areas, have to be facilitated.

The present study includes a diversity of topics. With the demand of including the most important aspects of changes in species composition due to changes in the land use regimes of an old agricultural landscape, it covers different methods from classical field work up to experiments in germination chambers.

2 Study area and study site “Dehesa San Francisco”

2.1.1 Study area

The study area is located in the foothills of the Sierra de Aracena y Picos de Aroche in northern Andalusia (south-western Spain). Due to topography and climate most of the area is used for pasture farming and wood and cork production. The climate is typical Mediterranean with hot, dry summer and mild, rainy winters. The mean annual temperature is 17.5°C with the coldest monthly mean temperature of 9,3°C in January and the hottest month with a mean temperature of 27°C in July. Mean annual rainfall is about 650 mm (Calama Sainz, 1997) with high interannual fluctuations between the years as well as within one year (Peco, 1989). The soils belonging predominantly to the soil type Terra rossa on shale (Calama Sainz, 1997).

Fig. 2.1: Map of Spain and Portugal. The flag points out the location of the “Dehesa San Francisco”, the study site of the present study.

The mountainous rim of Sierra Morena represents the southern slope of the Iberian Meseta and is, at the same time, the northern border of the study area. Altitude decreases from east to west, ranging from 1300m a.s.l., in Sierra Madrona or Sierra de la Estella, to 200 m at the western limits. The bedrock consists of siliceous lithological material, such as slates, granites and quartzes, with occasional Palaeozoic limestone outcrops (Giménez et al., 2004).

2.1.2 Study site

Field work has taken place at the farm "Dehesa San Francisco", a well-preserved dehesa (open woodland with *Quercus ilex* and *Quercus suber*), located 70 km north of Seville in the province of Andalusia (south-western Spain). The “Dehesa San Francisco” presents a typical farm in south-western Spain with traditional grazing with mixed herds (pigs, cattle and sheep) and pig fattening with acorns. It is covered with Mediterranean dehesa grasslands, sparsely, tree covered pastures with approximately 80 trees/hectare. The grasslands are extremely species rich annual grasslands. Therophytes form a predominant part, which is mixed with areas covered with changing fractions of several shrubs from the genus *Cistus* as well as *Genista hirsuta*, *Lavandula stoechas* and others.

The study site “Dehesa San Francisco” is situated in the extensions of the mountain region “Sierra de Aracena y Picos de Aroche”. Topography and climate allow in large parts only pasture farming respectively forest management (firewood and cork production). The area of the farm is subdivided by four mountain ranges extending from east to west, which is affecting the vegetation through strong micro-climatic differences (extreme hot and dry sunny southern slopes and moderate, shadowy northern-slopes). The altitude ranges from 360 m to 530 m and the climate is a Mediterranean climate with hot, dry summer and mild, rainy winter with 650 mm mean annual rainfall.

The farm “Dehesa San Francisco” is run by the Fundación Monte Mediterráneo, which bought the farm in 1995. Prior to that, the farm was about 200 years in family ownership. Until 1950, the families lived in small stone houses on the farm. Therewith, a traditional farming practice typical for the dehesa with ranging of cattle (about 30 – 50 cattle on about 1400 h) can be assumed. As the resource acorn was traditionally leased, pigs were brought onto the farmland in October for the acorn mast until February / March. After the 50`s, the families moved to the nearest village and the cultivation of the farmland decreased. In 1995, the Fundación Monte Mediterráneo started ecological livestock-breeding. In the first years the farming was focused on cattle breeding. In 1998 pig breeding of pure breed of Iberian pig started. Beneath cattle and pig ranging, a small herd of sheep (about 100) were kept on one pasture throughout the time.

Nowadays, ecological livestock breeding with cattle (Berenda and Retinta cattle), pigs (Iberian pigs), and in separated pastures sheep takes place with about 2.2 livestock units/hectare in mixed flocks on 700 hectares. The main focus of the exploitation lies on acorn mast of the Iberian pig for the production of the Jamón Ibérico de Bellota. Roughly 250 pigs were fattened on the farm annually until February. By the time of October the pigs enter the “montanera” or acorn fattening period with an age of more than one year and a weight of 100 kilos. Acorns, together with herbaceous pastoral growths, are the only fodder during the fattening periods. The only time in which the pigs stay in the stable is during birth and the rearing of the piglets. Therefore, due to fattening period and high pig numbers, the main use of pasture vegetation by pigs is from October until end of February. However, the most important factor for the mast is the effective use of the acorns, for which the pigs are moved during the fattening period in fast intervals using all areas of the farm. From June, the piglets born in spring are old enough for free ranging. However, due to the drought in summer, the rooting activity is limited to specific structures such as water holes. In addition to the pig grazing, the pastures are grazed year-round with cattle, with irregular rotations between the pastures. In summer 2002, formerly with mixed herds of cattle and pigs grazed pastures were divided into pastures which were grazed either by pig or by cattle and pig. A third treatment included abandonment. In August 2003, 200 hectares of the farm were destroyed by a natural bush fire. In order to reduce the fire risk the farm was ploughed, except of a few areas, directly after the fire hazard.

3 Effect of grazing on plant species composition of dehesa vegetation

3.1 Abstract

The dehesas in Spain and Portugal – descended from the Bosque mediterráneo, the Mediterranean hard leaves forest – are the result of a century long multi-factorial use by different livestock (e.g. cattle, sheep, goats and pigs), production of firewood and cork as well as extensive crop production. Due to a century-long grazing tradition, the vegetation of these very species-rich habitats seems to be well adapted to the removal of aboveground biomass as well as soil disturbances due to grazing livestock. However, the decline of open man-made habitats caused by abandonment and land use intensification represents a global problem. Sylvo-agropastoral systems like the dehesa are threatened through overgrazing, as in feed lots, or undergrazing, which results in growth of coarse vegetation and an increased thread of fire hazards. Both cause a decrease in biological diversity on habitat as well as species level.

Different grazing systems imply different disturbance regimes. These may effect species composition. Until now only cattle and sheep grazing and game browsing have been analysed for Mediterranean dehesa vegetation. In order to show the effect of different grazing regimes on vegetation, pig grazing, which has a long tradition in these grasslands, was analysed in the present work in addition to cattle grazing and fallow. Therefore, a formerly cattle and pig grazed pasture was divided into a continuously cattle and pig grazed pasture, a pig grazed pasture and fallow. Since habitat quality differed strongly at lower and upper slope, both sites were hence analysed separately. This experimental design represents a disturbance gradient regarding both the removal of aboveground biomass and soil disturbances.

The effect of the different grazing systems and fallow on vegetation is not only detected by species number in the present study, but also species composition. After four years, species number was highest on pig pasture, followed from cattle and pig pasture, and lowest at the fallow. Furthermore, species turnover was chosen as an indicator for diversity in order to analyse not only species number, but also the change in species composition. This development of species composition was identified using a detrended correspondence analysis.

3.2 Introduction

Grazing by domestic herbivores, which has a long tradition in the Mediterranean Basin, acted as a main driving force for the development of most Mediterranean ecosystems known nowadays. Grazing, often combined with wildfires, was one of the main factors for the conversion of Mediterranean forest into semi-natural grasslands and scrublands (Papanastasis, 1998). Dehesa grassland, developed through century long multi-factorial use with different livestock as well as extensive agricultural exploitation, includes some of the most species-rich communities outside the tropics (Marañon, 1986). According to Montoya Oliver (1989), the dehesa is one of the characteristic ecosystems of the Iberian Peninsula, with evergreen oak trees scattered in open savannah-like grasslands.

Basically, traditional management practices of a dehesa consist on free ranging of mixed herds of cattle, pigs, sheep, goats, and horses. Nowadays, vegetation in the Mediterranean Basin seems to be well adapted to grazing. Due to changing conditions for agricultural production (mainly in the 20th century), many dehesas were either abandoned or their management systems were simplified through specialisation of production on single types of use. Both lead to a decrease in the diversity of habitats and landscapes (Lavado Contador et al., 2000). Peco et al. (2006) studied the effect of abandonment from cattle grazing on species diversity and soil conditions in a Spanish dehesa in the Sierra de Guadarrama north of Madrid. Comparing not only cattle grazing and abandonment, but also upper and lower slope zone, both the grazing system and the slope zone were found as being influential on the vegetation.

In the present study, the approach of Peco et al. (2006) was modified. For this, pig grazing, as a typical grazing system of a traditional managed dehesa in the south-western part of Spain was added to the approach with cattle grazing and fallow. Due to the traditional grazing system of the dehesa, the cattle pasture was grazed in the present study with cattle and pigs in mixed herds. However, only areas were chosen with a negligible influence of pig pasturing on vegetation due to the activity radius of the pigs. Thus, with the present study, a gradient of disturbance regarding the aboveground vegetation and soil was considered. Here, the removal of aboveground biomass ought to be strongest on cattle and pig pasture, followed by pig pasture and lowest on fallow. In contrast, the disturbance of soil ought to be highest on pig pasture, followed by cattle and pig pasture and again lowest on fallow (Fig. 3.1). The expected change in position of cattle and pig pasture and pig pasture regarding the disturbance of aboveground vegetation and soil is based on the specific grazing behaviour of both livestock species. Cattle have a more intense grazing behaviour with soil disturbance mainly through trampling, whereas pigs have less impact on vegetation through grazing but higher impact on soil due to digging. The different disturbance regimes may cause differing functional adaptations and therefore may determine species composition.

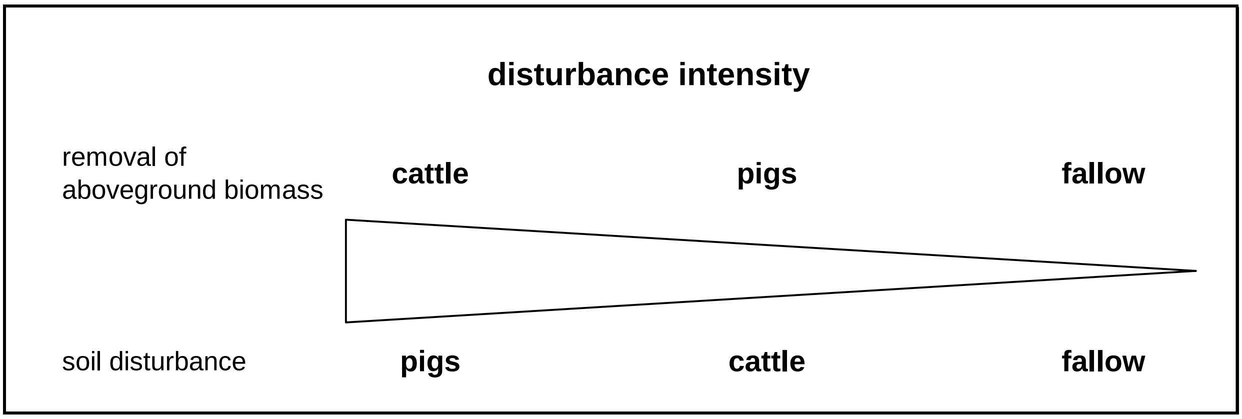

Fig. 3.1: Assumed disturbance gradient regarding aboveground vegetation and soil from cattle and pig pasture, pig pasture and fallow. Arrows indicate the intensity of disturbance.

Therefore, the impact of different grazing regimes, which represent a disturbance gradient both regarding aboveground biomass and soil, on species composition was studied in the present study. In order to show the differing effects of grazing regime in relation to a location factor, gradient in means of upper and lower slope zone was incorporated further-more.

3.3 Material and Methods

3.3.1 Vegetation relevés in permanent plots

The field work was carried out on the Dehesa San Francisco, which is described in chapter 2. The study area was grazed in low intensities (~0.5 livestock units / hectare) with mixed herds of cattle and pigs throughout the year. In summer 2003, the grazing system of the dehesa was partly re-arranged. A formerly cattle and pig grazed pasture was divided into i) continuously grazed cattle and pig pasture, ii) pig pasture and iii) fallow (Tab. 3.1). On the cattle and pig pasture, if considered over the whole year, pigs have only a small influence on vegetation compared with cattle grazing due to their limited activity radius. Since habitat quality differed strongly at lower and upper slope, permanent plots were installed at both sites (gradient 0-15 % and >15 %). Furthermore, all plots were situated in between the trees in the non-shadowed areas in southern slope without shrub encroachment.

In summer 2003, vegetation relevés of 2x2 m² were marked permanently with iron pickets. Each year from 2003-2006 sampling took place in April / May and was additionally controlled in the beginning of June in order to include also late growing species. Vegetation cover was estimated according to the method of Schmidt-Londo (Dierschke, 1994) with a nomenclature following Valdés et al. (1987).

Tab. 3.1: Number of vegetation relevés per treatment and year.

	upper slope zone			lower slope zone		
	cattle & pig pasture	pig pasture	fallow	cattle & pig pasture	pig pasture	fallow
vegetation period 2004	8	8	8	8	8	8
vegetation period 2005	8	8	8	8	8	8
vegetation period 2006	8	8	8	8	8	8

3.3.2 Data analysis

Average species number from the permanent plots of the collection of each year and treatment were calculated and were referred to single permanent plots. Species turnover (T) was calculated for every permanent plot between each consecutive year, using the formula following Mühlenberg (1993):

$$T = \frac{J + E}{S_1 + S_2} = \frac{S_1 + S_2 - 2G}{S_1 + S_2}$$

S_1 number of species in year 1
S_2 number of species in year 2
J number of species, which newly accrued in this permanent plot from year 1 to year 2

E number of species, which could not recovered in the second year
G number of shared species in both years

In order to show the vegetation development after the change in grazing management, a detrended correspondence analysis (DCA) was additionally applied. All vegetation samples from the years 2003 - 2006 were incorporated in the analysis. The development of the vegetation relevés are indicated with arrows.

3.4 Results

3.4.1 Vegetation development over time

The change in grazing regime is reflected by species number as well as species turnover rates. Fig. 3.2 shows annual average species numbers of the vegetation relevés from cattle and pig pasture, pig pasture and fallow from both upper and lower slope zone. Displayed are the years 2003 to 2006.

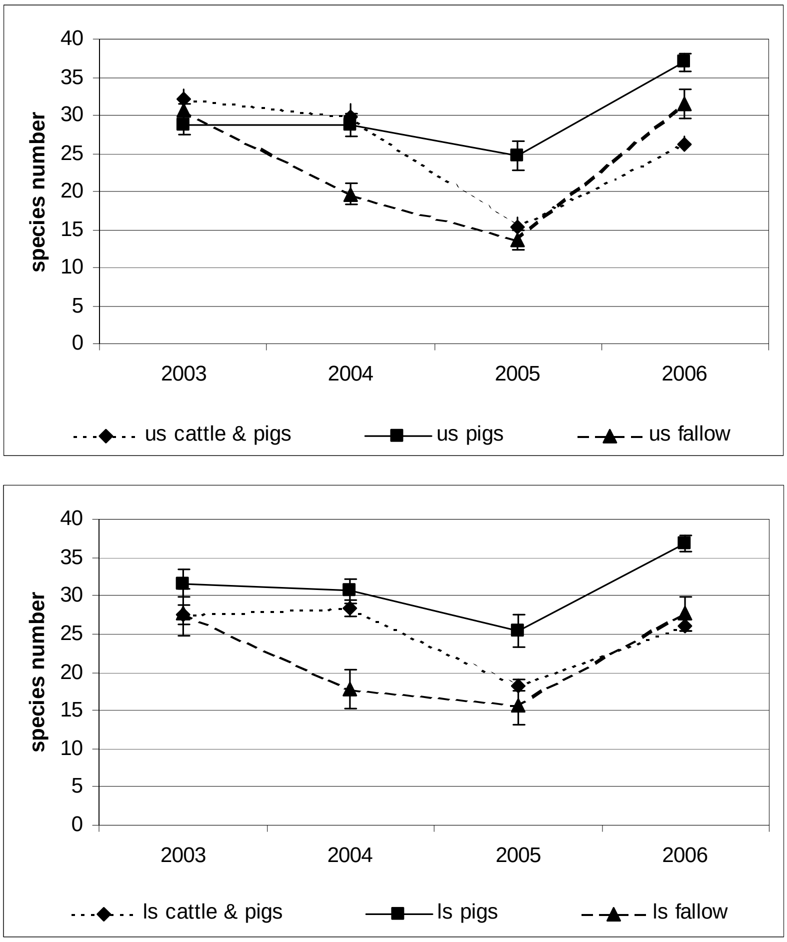

Fig. 3.2: Average species number per vegetation relevé from upper slope (upper figure) and lower slope (bottom figure), each from cattle and pig pasture, pig pasture and fallow (each number of relevé per pasture = 8) from the year 2003 to 2006. For each value, standard errors are indicated.

With about 30 species per vegetation relevé approximately the same number of species was mapped in the first year for both the different treatments and slope zones. Average species numbers in vegetation relevés of pig pasture increased in total and are higher than in cattle and pig pasture and fallow in the following three years. Average species number in vegetation relevés of the fallow was lowest until 2005, and then exceeded species number from cattle and pig grazed pastures. Contrary, average species numbers in vegetation relevés from cattle and pig pasture decreased slightly in total until 2006. In 2005, species number strongly decreased in all pastures both in upper and lower slope zone.

Vegetation relevés from fallow, which had the lowest average species number, showed in the analysis of species turnover highest values compared to cattle and pig and pig pasture for both upper and lower slope zone (Tab. 3.2). Species turnover values from cattle and pig pasture varied between 0.37 and 0.57 with differences between the years and slope zones. In lower slope zone, species turnover values from pig pasture was, mainly from 2003 – 2004 but also in both following years, higher than from cattle and pig pasture.

Tab. 3.2: Species turnover values ± standard error from permanent plots situated in upper and lower slope zone calculated following Mühlenberg (1993). All pastures were previously grazed with cattle and pigs. In summer 2003, the pasture was divided into cattle and pig pasture, pig pasture and fallow.

	upper slope			lower slope		
	cattle & pigs	pigs	fallow	cattle & pigs	pigs	fallow
2003-2004	**0,41** ± 0,03	**0,48** ± 0,03	**0,62** ± 0,04	**0,37** ± 0,02	**0,57** ± 0,02	**0,64** ± 0,05
2004-2005	**0,49** ± 0,04	**0,45** ± 0,02	**0,53** ± 0,03	**0,39** ± 0,02	**0,42** ± 0,02	**0,41** ± 0,04
2005-2006	**0,48** ± 0,03	**0,46** ± 0,03	**0,56** ± 0,03	**0,40** ± 0,02	**0,47** ± 0,03	**0,52** ± 0,04

Comparing species composition and similarity of the vegetation relevés, the differently grazed pastures had, divided in upper and lower slope zone, a high conformity in the first year of exploration (Fig. 3.3). After the change in grazing system in summer 2003, species composition changed. However, the influence of slope remains clearly visible throughout the years. Slope zone is described through axis 2, which explains about 22 % of variance, whereas vegetation samples diverge and shift in space along axis 1, which explains about 37 % of variance. Throughout all four years of the study, the order of the vegetation relevés from the differently grazed areas, both in upper and lower slope zone, remained the same: left hand side the vegetation samples from cattle and pig pasture, right hand side from the fallow, and in between the permanent plots from the pig pasture. The strong influence of the dry year 2005 on species composition throughout all pastures is also clearly visible in Fig. 3.3.

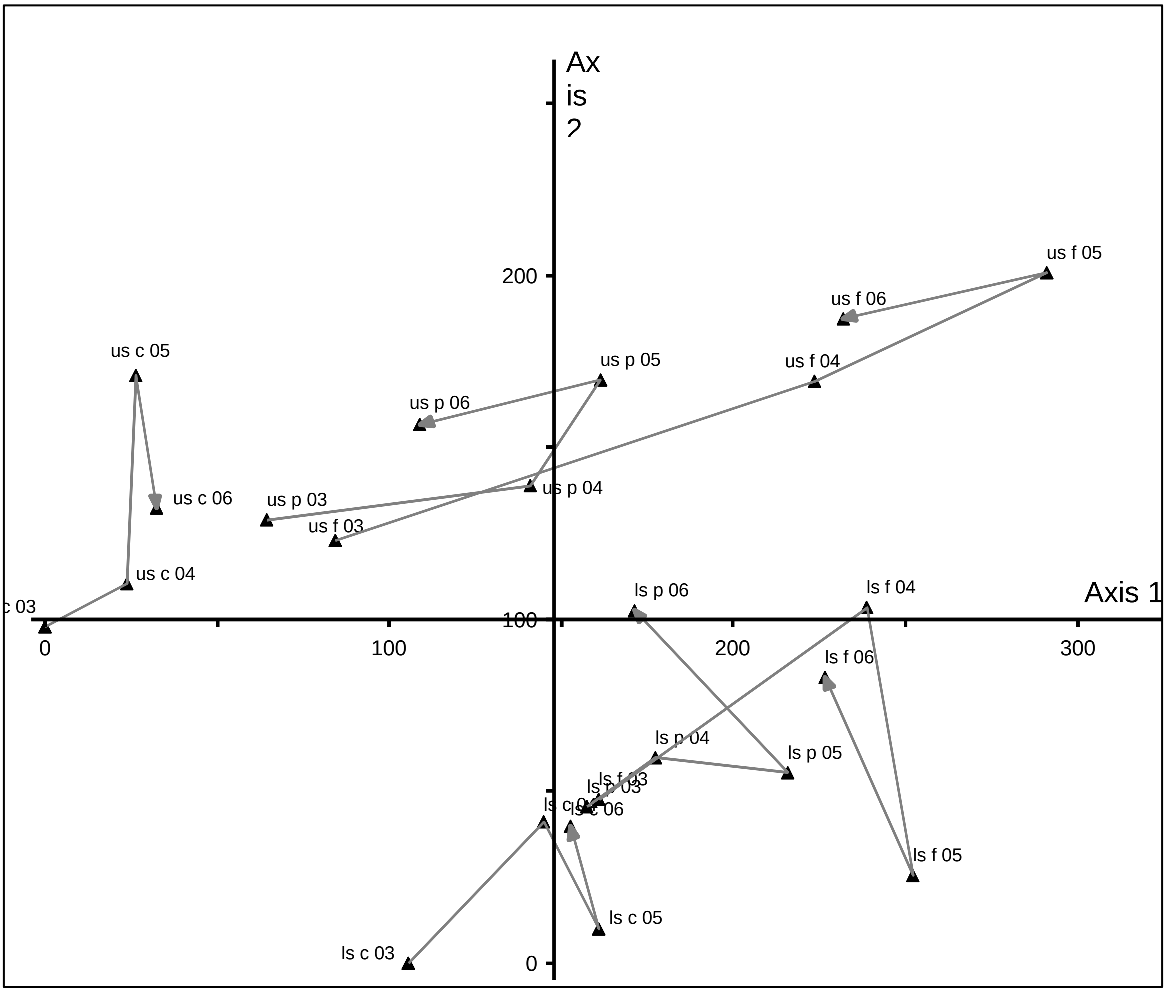

Fig. 3.3: Detrended Correspondence Analysis (DCA) of species abundances of differently grazed areas. Species abundance is implemented as percentage of species cover in the permanent plots. Changes over time are marked with arrows, beginning in the first vegetation period after installation of the pastures (2003) and ending four years later in 2006.First two letters give the slope zone with us = upper slope and ls = lower slope. Single letters give the pasture type with c = cattle and pigs, p = pigs, and f = fallow.
Numbers give the year of vegetation samples from 03 = 2003 up to 06 = 2006.
Axis 1 explains 36.8% of variance, axis 2 explains 22.2% of variance.

3.5 Discussion

In the present study, species number on pig pasture increased over the years. The vegetation on cattle and pig pasture, which presented the unaltered pasturing system, showed only small changes. On the other hand, species number on fallow decreased over the years. These results match with studies about grazed and un-grazed areas, which usually detect increasing plant diversity on grazed areas (e.g. Hill et al., 1992; Humphrey & Patterson, 2000; Sánchez et al., 2001). Furthermore, an increase in species number was also found in digging places of wild pigs in Central Europe (Treiber, 1997) as well as in an experimental pig pasture in the floodplain of the Elbe river (Micklich, 1996). With the disturbance of normally dense vegetation through the digging, grazing, and trampling of the pigs, patchiness increases. This leads mostly to an increase in plant diversity (Fensham et al., 1994; Micklich et al., 1996; Treiber, 1997; Beinlich, 1998). Both, species from actual vegetation as well as from soil seed bank get opportunities for germination (Micklich et al., 1996; Beinlich, 1998; Poschlod & Ittel, 2005). Through digging, new niches and different successional stages are created, providing a mosaic of micro – sites. With this, not only species diversity increases, but, above all, low competitive species are facilitated. Beneath the removal of aboveground biomass, cattle grazing also create small disturbances of the sward through trampling. However, cattle grazing created, compared to pig grazing, a more or less even and short vegetation. On fallow, accumulation of aboveground biomass leads to competitive exclusion and accumulation of litter. Both result in a prevention of germination of ephemeral species, which involves decreasing species numbers (Milton et al., 1997; Neugebauer, 2004). However, in the present study species number increased again in the last year of the study on the fallow. This may be caused by an increase in mouse activities (own observation). The vegetation free mouse paths in the exclosures may have formed germination niches in the formerly dense vegetation of the fallow with subsequently increasing species numbers. The especially dry year 2005 was also reflected in a decrease in species number over all pastures from both upper and lower slope zone. The influence of drought on species composition is also shown in chapter 4.

Beneath disturbances, differing fodder selectivity may influence species composition on pastures (Reyneri et al., 1994), too. With higher grazing pressure on palatable species and therewith decreasing competitiveness of these species, toxic and less palatable species may increase in abundance and cover on grazed grasslands (Wehsarg, 1954). As grazing with mixed herds of cattle and pigs has a century long tradition in dehesa grasslands, selection of species due to palatability has to be assumed in these ecosystems.

Whereas pig pasture had the highest species number compared with both others, fallow showed the highest change in species composition to be revealed by species turnover values of up to 0.64. With species turnover values between 0.37 and 0.64 through all years and pastures, the values in the present study are in general high compared e.g. with results from Neugebauer (2004) for differently used pastures in Central Europe. Here, values between 0.2 – 0.35 were found for areas grazed with pigs and from 0.14 – 0.35 for fallows. The Mediterranean vegetation is known for its high variation in species composition from one year to another, mainly induced by strongly differing rainfall between the vegetation periods (Figueroa & Davy, 1991). Natural population dynamics can lead to surprisingly high species turnover rates even in long standing meadows (Berlin et al., 2000). Even those areas with low species numbers may have high species turnover with an exchange of species from one year to another. In contrast, areas with a high species number could be in a stable state without numerous species exchanges, like it is expected for the evenly grazed cattle pasture (Briemle, 1987).

Natural population dynamics means non-directed change in species composition. The analysis of vegetation development and similarity of species composition from the differently grazed areas over the years points out that the high turnover rates comprise, beneath natural vegetation dynamics, also a directional part. Vegetation composition changed after the change in grazing system. The permanent plots from the same pasture showed close similarity regarding their species composition. In all four years of observation, the general arrangement of permanent plots has cattle and pig pasture on one end, pig pasture in the middle and fallow on the other end. This arrangement was congruent over both upper and lower slope zone. Also the dry year 2005 was seen in the development of the differently grazed pastures.

However, low-intensity grazing has not only impact on vegetation structure and composition, but also on physical and hydrological properties, affecting species composition furthermore (Peco et al., 2006). This was also found in the present study with an impact of grazing regime not only on species composition, but also on soil humidity in differently treated pastures (chapter 4). In addition, these changes in species composition as well as physical and hydrological properties may have important consequences for the conservation of these often very valuable grazed grasslands (Peco at al., 2006).

Given that most of the plants die in early summer in Mediterranean dry grasslands and regular grazing avoid accumulation of litter, micro-sites for germination are usually not the limiting factor for germination in grazed Mediterranean dehesa vegetation. Therefore, the increase in bare soil through the digging of the pigs, which is important in the dense vegetation of productive grasslands, may not have such an effect on germination in dry Mediterranean grasslands. Contrary, succession of the fallow leads to accumulation of litter and a decrease in bare soil, preventing germination of most of the species.

Thus, comparing the effect of pig pasture and fallow on germination of annual species, succession of fallow seems to change environmental conditions much stronger than pig pasturing does. In dry Mediterranean grasslands, exclusive pig pasturing causes a succession of the vegetation towards fallow, with a patchiness of short and high growing vegetation in variation with vegetation gaps. This development of the pig pasture is shown through the ordination of the vegetation relevés. In both upper and lower slope zone, pig pasture was always situated in between cattle and pig pasture and fallow. Therewith, an increase of species typical for fallow together with different successional stages in the digging patches amplifies the vegetation of the grazed pasture.

4 Effect of fire and ploughing on species composition of Mediterranean type dehesa vegetation

4.1 Abstract

Mediterranean dehesa vegetation seems to be well adapted to grazing livestock due to a century long grazing tradition. However, as most of the late successional species (e.g. *Cistus* spec., *Genista* spec.) possess chemical or physical defence mechanisms against grazing, both periodic ploughing as well as burning are traditionally applied for maintaining dehesa grasslands, and with it, to control unwanted shrub vegetation. Furthermore, due to missing efficiency in the management of marginal areas, abandonment displays a severe threat to the ecosystem dehesa. Thus, burning and ploughing are commonly used as subsidies for traditional farming systems in order to keep old, traditional landscapes open.

In the present study, the question has been addressed if the managements burning, ploughing and burning combined with ploughing, which imply severe disturbances both to the aboveground vegetation as well as to the soil, affect vegetation adapted to permanent grazing. Furthermore, it has been investigated whether these disturbances are triggering vegetation development toward a new species composition over a longer period or the vegetation is regenerating fast towards its previous state.

In order to identify the effects of these traditional treatments (burning, ploughing and burning combined with ploughing) on species composition, a vegetation study was accomplished using as a reference continuously grazed areas (mixed herds with pigs and cattle) without further management. As a result, species composition as well as species number differed both between the differently managed areas as well as between those areas, which were managed and those, which were only grazed. Based on the question if different managements as well as slope zone influences soil moisture and its effect on species composition, an analysis of soil moisture of the differently used areas was incorporated in the present study, too. Soil moisture of differently managed areas as well as zones with different slope were analysed regarding species composition and species number. From this it was shown that management has a strong influence on water capacity of soil as well as species composition and species numbers. Furthermore, the influence of management on shrub encroachment was studied. *Cistus* spec. as typical phryganic plants from the Mediterranean Basin showed an increase on the burnt and burnt and ploughed areas compared to the ploughed and grazed pastures, indicating the management problems of encroachment of these unwanted shrubs after fire hazards.

4.2 Introduction

The dehesas in Spain and Portugal are descended from the bosque mediterráneo, as the result of a century long multi-factorial use (Hampe, 1993; Montero et al., 1998). In this climatic zone, the Bosque mediterráneo, the Mediterranean hard leaves forest (Rivas-Goday & Rivas-Martínez, 1963) covered huge areas from Andalusia, and is now reduced to small, for human hardly accessible areas. Whereas the better, deeper soils are cultivated for crop production periodically in cycles of 4-5 years, grazing usually predominates with mixed herds of cattle, sheep, goats and pigs on the shallower soils and the steeper slopes. Due to the century long grazing tradition, vegetation in the Mediterranean dehesa is well adapted to grazing livestock (Azcárate et al., 2002; Peco et al., 2005). In the Mediterranean dehesa, most of the common, late-successional species (e.g. *Cistus* spec., *Lavandula* spec., *Genista* spec.) possess physical or chemical defences against grazing. Therefore, periodic ploughing (Sánchez et al., 2001), or in former times also occasional burning (Figueroa & Davy, 1991), is traditionally used in order to control undesired shrub vegetation on the grasslands.

Frequently ploughed areas own a special flora due to the requirements created through the removal of aboveground biomass together with soil disturbances (Austrheim & Olsson, 1999). Mainly annual, small, and low competitive species from naturally disturbed habitats found an alternative habitat on extensively used agricultural areas. As well as ploughing, frequent burning admits the development of special, adapted vegetation. This is already shown in many studies especially for Mediterranean vegetation (Naveh, 1975; Trabaud & Lepart, 1980; Arianoutsou & Margaris, 1982), as well as for other vegetation types (Keeley, 1991; Bylebyl, 2007; Schreiber et al., 2000). Walter (1968) identified fire as one of the major ecological factors which shaped the Mediterranean landscape and affected its present mosaic-like pattern of regeneration and degradation stages. Since natural as well as by human started fires were shaping Mediterranean landscapes decisively over centuries (Trabaud 1994, 2002), many species have evolved strategies in order to survive periodic fires (Naveh, 1975; Pausas, 1999a). Due to human impact, the frequency of fire recently increased in the Mediterranean Basin and is expected to further increase as a result of global climate change in all Mediterranean type ecosystems (Beer & Williams, 1995; Pausas, 1999b; Pausas, 2004; Pausas et al., 2004). According to Pérez & Moreno (1998), more than 200,000 ha, of which 41.2% were woods, have been burned each year in Spain over the last few decades.

Besides the management type, the vegetation development in the Mediterranean dehesa is mainly influenced by the Mediterranean climate. In the Mediterranean Basin, the climate is known for the high oscillations of precipitation within one year as well as over the years (Figueroa & Davy, 1991). In combination with high temperatures in summer, the Mediterranean climate acts as a filter for plant traits in order to ensure the survival of plant species. Therefore, especially the variation in rainfall during germination season has a strong impact on species composition in Mediterranean ecosystems (Marañon & Bartolome, 1989; Peco, 1989; Figueroa & Davy, 1991; Clary, 2008). However, Landsberg et al. (1999), and also McIntyre et al. (1999) found a modification of species reaction to drought through grazing and management system. Climatic conditions may act as filters on plant functional traits and therewith shift the relevance of plant traits for the adaptation to differing factors like climate and disturbances (Milchunas et al., 1989; Landsberg et al., 1999; McIntyre et al., 1999; Sternberg et al., 2000; de Bello et al., 2005; Clary, 2008).

In order to study the effect of different managements on the vegetation of a Mediterranean habitat adapted to a traditional grazing system, a vegetation study was accomplished in Mediterranean dehesa grassland. Parts of the dehesa were affected by a natural fire and have been ploughed afterwards. Adjacent to these areas, continuously grazed areas without any further management were used as a reference. With this setting, the following questions have been addressed:

- How do single managements like burning and ploughing, which implies severe disturbances both to the aboveground vegetation as well as to the soil, affect the vegetation adapted to permanent grazing?
- Do these disturbances trigger vegetation development toward a new species composition over a longer time period or do the vegetation regenerate fast towards their previous state?

In this context, also the influence of management on shrub encroachment was studied, too. Based on the question if different managements as well as slope zone influence soil moisture and its effect on species composition, an analysis of soil moisture of the differently used areas was incorporated in the present study, too.

4.3 Material and Methods

4.3.1 Vegetation relevés in permanent plots

The field work was carried out on the Dehesa San Francisco, which is described in chapter 2. In summer 2004, a natural fire burned parts of the study area. With few exceptions, the whole area was ploughed directly after the fire hazard. In order to monitor the vegetation development, permanent plots were marked on freshly ploughed, burnt and burnt and ploughed areas. As reference areas, permanent plots from cattle and pig pasture without further management were incorporated in the present study (Tab. 4.1). These pastures were directly adjacent to the burnt and ploughed areas. All areas were grazed before and during the monitoring with mixed herds of cattle and pigs in low intensities (~0.5 livestock units / hectare). Since habitat quality differed strongly at lower and upper slope, permanent plots were installed at both sites (0-15 % gradient and >15 % gradient) for cattle and pig pasture and ploughed pasture. The burnt and burnt and ploughed pastures were restricted to the lower slope zone. In order to ensure the comparability of the vegetation relevés, all plots were chosen in between the trees in the non-shadowed areas in southern slope. In 2005, a special dry vegetation period occurred with about 60% less vegetation cover than in the year 2004 due to missing rainfall.

Tab. 4.1: Number of vegetation relevés per treatment and year.
* The reduction of vegetation relevés in some management types are caused by the loss of markings due to the grazing livestock.

	ploughed, upper slope	ploughed, lower slope	burnt, lower slope	burnt & ploughed, lower slope	cattle & pig pasture, upper slope	cattle & pig pasture, lower slope
vegetation period 2004	10	10	10	10	8	8
vegetation period 2005	10	10	9*	7*	8	8
vegetation period 2006	10	10	8*	6*	8	8

Each year from 2004 - 2006 sampling took place in permanently marked vegetation relevés of 2x2 m² in April / May, and again in the beginning of June in order to include also late growing species. Vegetation cover was estimated according to the method of Schmidt-Londo (Dierschke, 1994). Nomenclature followed Valdés et al. (1987).

4.3.2 Measurement of monthly rainfall

Precipitation was measured daily during three years (Fig. 4.1). For that, a measurement instrument for precipitation after Hellmann was used on the study site sheltered from wind and sun. Daily at 9 am the water level was noted and the content was emptied.

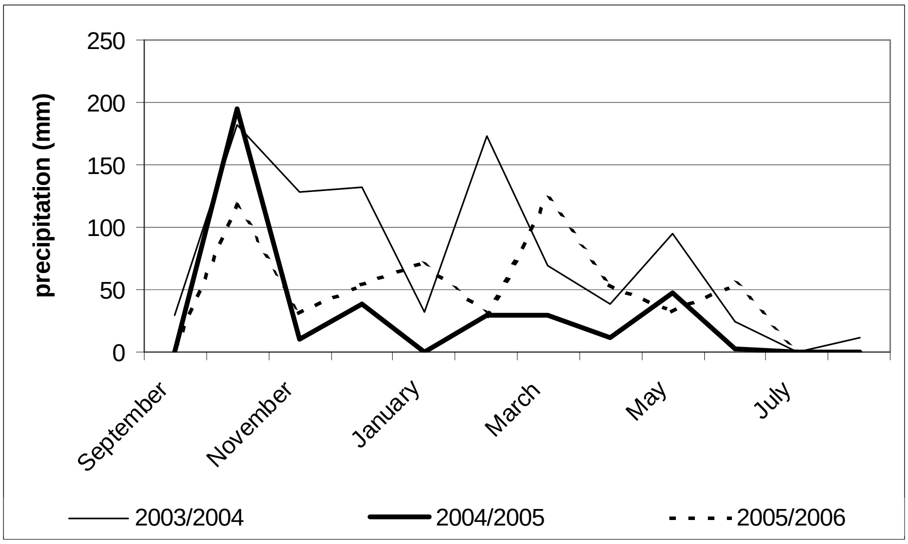

Fig. 4.1: Total monthly rainfall during the vegetation periods 2003 – 2006 measured daily at the Dehesa San Francisco. The thick line indicates the rainfall in the vegetation period 2005, in which rainfall was extremely low.

4.3.3 Measurement of soil humidity

In order to detect differences in loss of soil moisture due to the slope gradient as well as to the different management practices, the soil moisture was measured daily for ten days always in the morning in a period without precipitation after a strong rainfall. For the measurements, watermark sensors (type WMSM) were used. As watermark sensors need undisturbed soil for the measurements, the ploughed areas were omitted in the analysis of soil moisture. In order to increase the range of managements, pig pasture and fallow, both from upper and lower slope zone, were incorporated additionally in the analysis of soil moisture. For further information about the pastures and fallow see chapter 3.

4.3.4 Analysis

Overall differences in species composition were analysed by means of multivariate statistics. A detrended component analysis (DCA) was applied to analyse the similarity of the managed pastures and the grazed pastures without further management. Average species number from the permanent plots of one collection year and treatment were calculated. The temporal development of the vegetation relevés was indicated with arrows. In a second step a subsequent correlation of species abundance with the axes was conducted. Ordination analysis was conducted with PC-Ord 4.33. Besides the analysis of the herbaceous vegetation, the shrubby vegetation of the study site has been analysed separately to show the impact of different management types on shrub encroachment. For this, frequency and abundance of *Cistus* spec. (*Cistus crispus, Cistus ladanifer, Cistus salviifolius)* as typical phanerophytes were analysed. For the analysis of frequency the plots with *Cistus* spec. per year and management were summarized, whereas for the abundance the average cover of *Cistus* spec. over all vegetation relevés of one year and management was calculated.

4.4 Results

The influence of the different managements on species composition is shown in Fig. 4.2 with an ordination of vegetation relevés from all managed pastures together with cattle and pig pasture from upper and lower slope zone. The influence of the dry year 2005 is described through axis 2, which explains about 26 % of variance. After the strong influence of the year 2005 with a clear separation of the vegetation relevés, species composition from the vegetation relevés from the year 2006 resembles the ones from 2004 from the cattle and pig pasture both for upper and lower slope zone. The burnt, ploughed and burnt and ploughed areas developed, after the divergence along axis 2 in 2005 due to the drought, along axis 2, which explains about 45 % of variance. The cattle and pig pasture from lower slope zone is clearly separated from the other managed pastures through axis 1, and the managed areas developed in the opposite direction. The cattle and pig pasture from upper slope zone is clearly separated through axis 2, which express for all other managements the influence of the dry year 2005. Using a subsequent correlation of species abundance with the axes, most of the species were correlated with the cattle and pig pasture from lower slope zone. As cattle and pig pasture from upper slope zone as well as the influence of the dry year were described through axis 2, the correlation of the second large proportion of species along axis 2 could not be assigned to any management or precipitation.

The analysis of species number showed differences between the differently treated areas (Fig. 4.3). Species number of the grazed plots from upper and lower slope zone showed only minor changes throughout the investigation period with being lowest in the dry year 2005. The same, relatively constant species number with a drop in 2005 was shown also on the permanent plots from the ploughed, lower slope zone as well as the burnt and burnt and ploughed area. The impact of the additional ploughing is reflected only in a slightly reduced species number in the first year after burning and ploughing, which was taken up again in 2006. In contrast, in the ploughed, upper slope zone species number was obviously lower in 2004, the first vegetation period after ploughing, but increased in the following years even in the dry year 2005. The negative impact of the dry year on species number was strongest on the burnt and burnt and ploughed pastures compared with the other areas. In 2006 the differences in species number were negligible throughout the treatments.

Water tension increased strongest in the soil from the cattle and pig pasture, upper slope zone and the burnt and burnt and ploughed pasture (Fig. 4.4). At the end of the measurements, also cattle grazed, lower slope zone reached just as high tensions. Both upper and lower slope zones from pig pasture and fallow showed a moderate rise in tension until the end of the measurements.

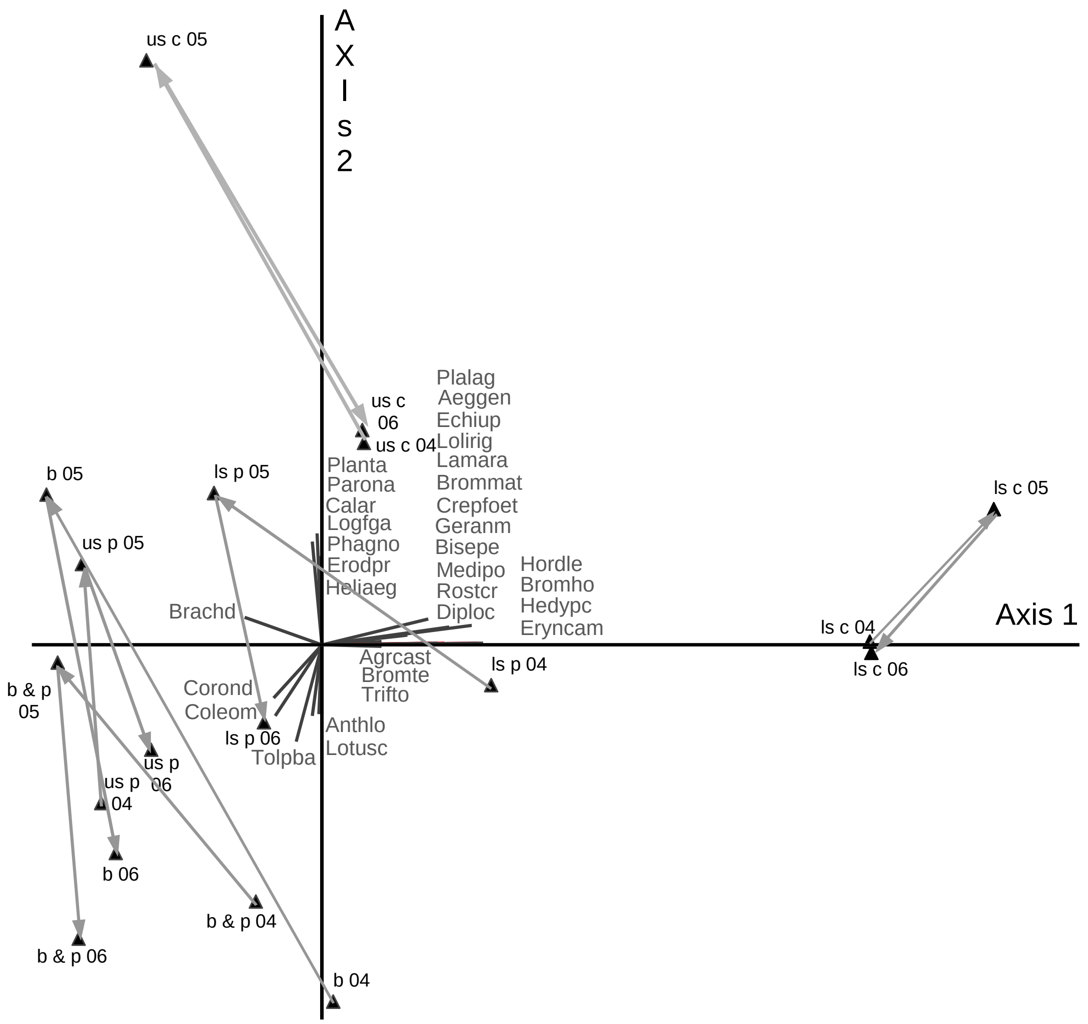

Fig. 4.2: Detrended Correspondence Analysis (DCA) of species abundances of ploughed, burnt, and burnt and ploughed areas as well as cattle and pig pasture without further treatments from upper and lower slope zone. Species abundances is implemented as percentage of species cover in the vegetation relevés. Changes over time are marked with arrows, beginning in the first year after burning and ploughing (2004) and ending three years later in 2006. Included is species cover of the permanent plots as matrix 1. Cut-off value >0.3. Axis 1 explains 44.8 % of variance, axis 2 explains 26.2 % of variance (Relative Euclidian distance).

Abbreviations: us c(04/05/06) = upper slope, cattle and pig grazed (year); ls c(04/05/06) = lower slope, cattle and pig grazed (year); us p (04/05/06) = upper slope, ploughed (year); ls p (04/05/06) = lower slope, ploughed (year); b (04/05/06) = lower slope, burnt (year); b & p (04/05/06) = lower slope, burnt and ploughed (year); Aeggen: *Aegilops geniculata*; Agrcas: *Agrostis castellana*; Antlot: *Anthyllis lotoides*; Bispel: *Biserrula pelecinus*; Bradys: *Brachypodium distachyon*; Brohor: *Bromus hordeaceus*; Bromat: *Bromus matritensis*; Brotec: *Bromus tectorum*; Calarv: *Calendula arvensis*; Colmyc: *Coleostephus myconis*; Cordur: *Coronilla dura*; Crefoe: *Crepis foetida*; Dipcat: *Diplotaxis catholica*; Echpla: *Echium plantagineum*; Eropri: *Erodium primulaceum*; Erycam: *Eryngium campestre*; Germol: *Geranium molle*; Hedcre: *Hedypnois cretica*; Helaeg: *Helianthemum aegyptiacum*; Horlep: *Hordeum leporinum*; Lamaur: *Lamarckia aurea*; Loggal: *Logfia gallica*; Lolrig: *Lolium rigidum*; Lotcon: *Lotus conimbricens*; Medpol: *Medicago polymorpha*; Pararg: *Paronychia argentea*; Phasax: *Phagnalon saxatile*; Plaafr: *Plantago afra*; Plalag: *Plantago lagopus*; Roscri: *Rostraria cristata*; Tolbar: *Tolpis barbata*; Tritom: *Trifolium tomentosum*;

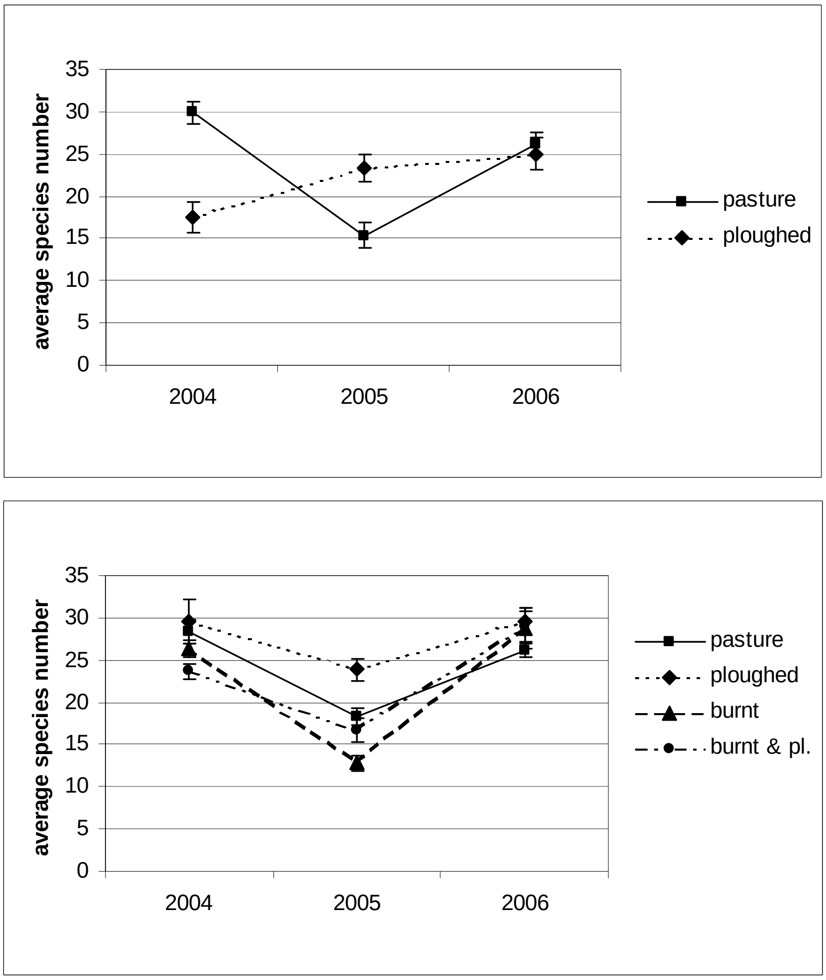

Fig. 4.3: Average species number of the differently managed areas, including the standard errors.
Top figure: cattle and pig pasture and ploughed pasture on upper slope zone. Bottom figure: cattle and pig pasture, ploughed pasture, burnt pasture and burnt and ploughed pasture, all from lower slope zone.

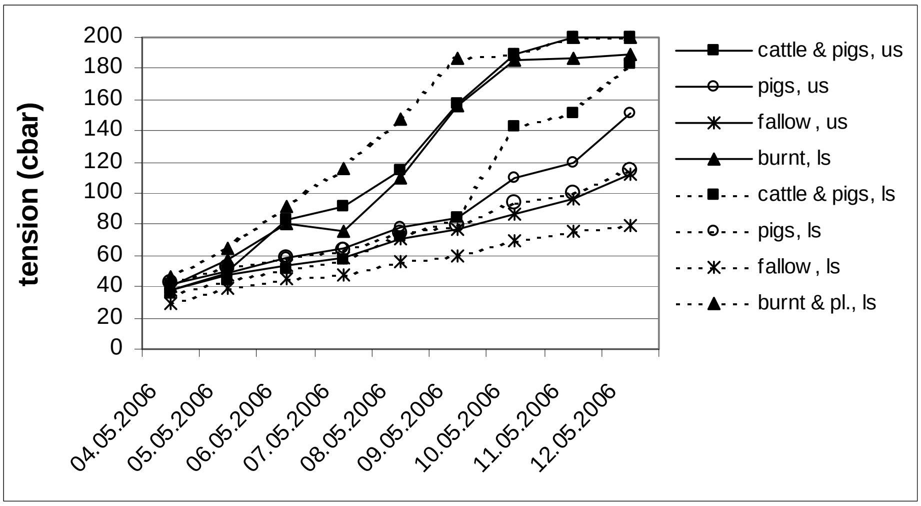

Fig. 4.4: Increase in water tension of soils from different areas from the study site. Measured was soil tension after a strong rainfall for ten days. Abbreviations: us: upper slope zone, ls: lower slope zone.

Frequency and cover of *Cistus* spec. varied already in the first year after the accomplishment of the managements in the year 2004 (Fig. 4.5). On the burnt and burnt and ploughed pastures, frequency was already high in 2004 with a moderate rise until 2006, whereas cover showed a steep increase from 2004 to 2006. Cattle and pig pasture from upper slope zone as well as the ploughed pasture both from upper and lower slope zone had, after low frequency and abundance in 2004, an increase in 2005 with decrease again in 2006. The cattle and pig grazed lower slope zone had no *Cistus*-growth at all.

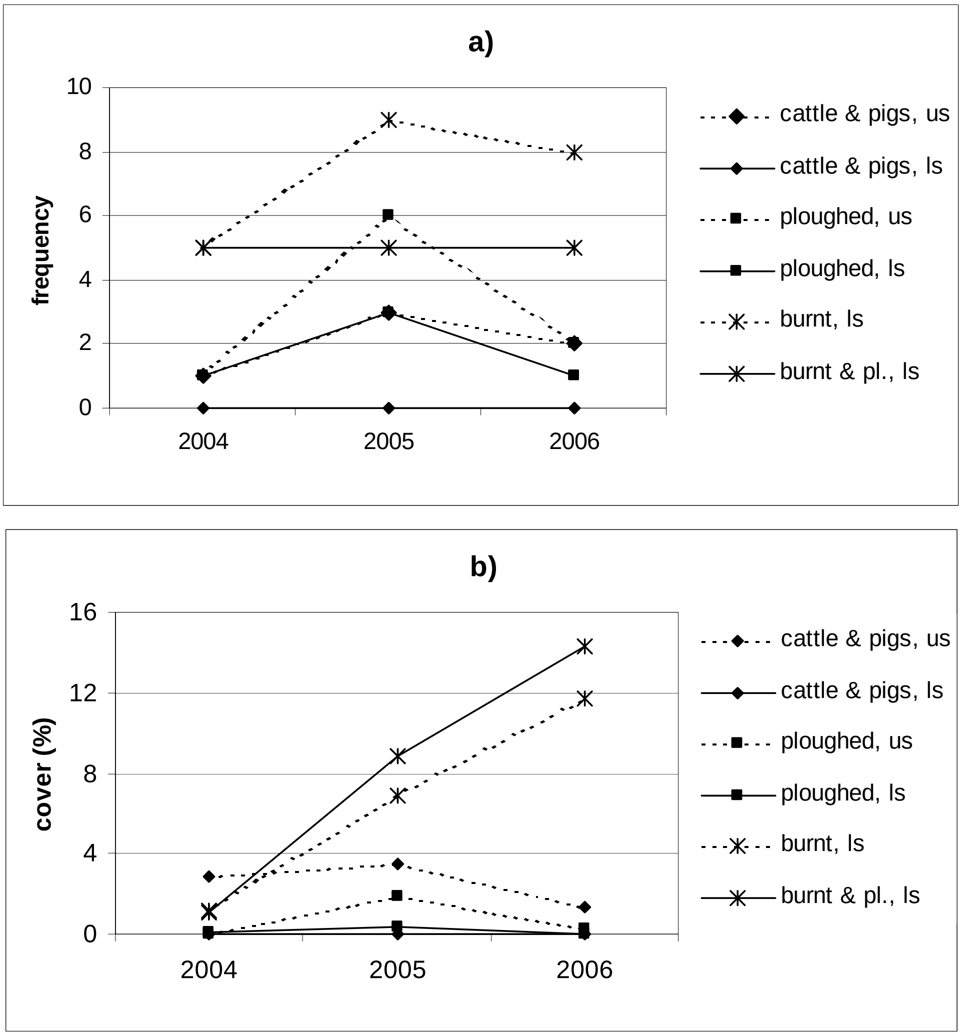

Fig. 4.5: Frequency (figure a)) and cover (figure b)) of *Cistus* spec. in vegetation relevés in differently managed areas from 2003 to 2006. Abbreviations: us: upper slope zone; ls: lower slope zone.

4.5 Discussion

In the present study, different managements affected species composition of Mediterranean dehesa vegetation. The vegetation relevés from the cattle and pig pastures without further management were clearly separated in the ordination from the additional managed areas. Whereas all areas were permanently grazed with mixed herds throughout the year, the management treatments burning, ploughing and burning and ploughing included additionally the total removal of above-ground biomass and, with ploughing, furthermore the disturbance of soil. Through all three years of investigation, vegetation was more similar in between the managed areas than between the managed areas and the grazed areas. The ploughed and ploughed and burnt area showed the furthermost distance to the grazed area in terms of species composition. Therewith, the question raises if the differences in species composition between the managed areas and the grazed areas without further management are due to the short investigation period and vegetation would match again in the following years. If this would not be the case and direction of succession deviates from the expected, could it be then explained by mechanisms activated through the additional disturbances? Regarding this, the question about ongoing succession was addressed by Bernaldez (1991) and Chytrý et al. (2001) in their studies about succession after different disturbances respectively cessation of ploughing. Both found increasing species number for a time period longer than three years after the last ploughing. This would predict ongoing succession on the ploughed and burnt areas for some more years. Also Sebastiá & Puig (2008) acknowledged the fast recovery after ploughing in different mesic grassland, but also mentioned a kind of memory of past events through the long persistence of plants found in all ploughed areas long after the disturbance was made.

As both burning and ploughing affect, besides the above-ground vegetation, also soil seed bank, an influence on species composition in these areas due to an enhanced germination rate from soil seed bank can be assumed (McDonald et al., 1996; Pywell et al., 1997). The high percentage of annual species in Mediterranean grassland (e.g. Marañon, 1991), depending on seed germination each year after the dry summer, should contribute additionally to an increase in species number after the removal of aboveground biomass. Furthermore, after a fire, the low competition after the total deletion of aboveground biomass offers good growing conditions for many post-fire seeders such as therophytes, and for post-fire resprouters, such as many woody plants. Additionally, post-fire sites often provide enhanced nutrient supply (Buhk et al., 2007). Germination from soil seed bank after fire depends not only on seed numbers present in soil at the time of fire, but also on their survival ability, their germinability after fire and subsequent seedling survival in an environment changed after fire (Moreno & Oechel, 1994). Even seeds of opportunistic species (like *Asterolinum linum-stellatum* or *Dipcadi serotinum*) have been known to survive extreme heat very well (Moreno & Oechel, 1991; Bell & Williams, 1998; Buhk & Hensen, 2006). However, the expected increase in species number on the burnt areas compared to the only grazed areas due to germination stimulation was not found in the present study, although heat-shock stimulated germination is widespread in many plant families and is found in many ecosystems (Christensen & Muller, 1975; Arianoutsou & Margaris, 1982; Kelly et al, 1992; Herranz et al., 1998), as well as smoke triggered germination (Dixon et al., 1995; Keeley & Fotheringham, 1998; Bylebyl, 2007; see also chapter 7).

However, the removal of aboveground biomass through ploughing or burning may not have the effect of enhancement of biodiversity in Mediterranean type grasslands dominated by annuals as it is known for grassland types dominated by perennial species (e.g. Bullock et al., 1994). Due to the commonly dry summer in this region and with this, the die back of most of the plants together with permanent grazing pressure, gaps in vegetation for germination with the beginning of the vegetation period should not be the limiting factor in dry Mediterranean grasslands. Furthermore, the upper 5-10 cm of undisturbed soil may already dry out within 5-25 days in arid climates (Noy-Meir, 1973). Therefore, most of the seedlings with too short roots for water supply from deeper soil layers would die, even in an adequate humid vegetation period. Additionally, because of the endangerment of soil sealing, and with this the enhanced jeopardy of soil erosion by wind and water of the desnuded soil, abandoned fields are often unfavourable for germination and development of new vegetation (Pausas, 1999 a; Hammouda et al., 2003).

Water loss after a strong rainfall in differently managed areas both from upper and lower slope zone revealed strong differences due to management of the area, but also due to slope. Given that water capacity is nearly the same at the beginning of the measurement after a rainfall, the faster loss of soil humidity seems to be caused by reduced protection against evaporation. Higher transpiration from plants seems to play a minor role compared to reduced evaporation due to shading through vegetation. The relatively low species number of the ploughed, upper slope zone compared with the respectively grazed areas can be interpreted within the context of different degrees of moisture due to gradient and vegetation structure. Therefore, the burnt and ploughed areas dried out fastest, followed from cattle grazed upper slope zone with patchy and short vegetation. The burnt and cattle grazed lower slope also showed a fast increasing tension. Intermediate rise of tension was measured for the pig grazed upper slope. A moderate rise was recorded for the pig grazed lower slope together with the upper slope fallow and the area with the lightest tension at the end of the measurement was the fallow in lower slope zone. Summarized, the denser and higher the vegetation, the lower the loss of humidity. Therefore, a change in vegetation structure due to a change in management system also influences plant growth through a change in soil humidity (Bojie et al., 2000; Altesor et al., 2006).

Besides species number, also species composition was affected through drought in the year 2005. Average vegetation cover during the vegetation period 2005 was about 60% less than in the year 2004 due to missing rainfall. Many species emerged in lower abundance and cover and died before setting flowers. Whereas the cattle and pig grazed areas returned approximately to the state before the dry year, the managed areas developed furthermore. In 2006, the last year of observation, the ploughed, burnt and burnt and ploughed areas were more similar than in the first year after the management, which took place in 2004. High species dynamic with large variations in floristic composition was found in several studies in annual grassland in the Mediterranean, which was mainly contributed to fluctuations in total annual rainfall and its distribution over the year (Peco, 1989; Figueroa & Davy, 1991). Many studies acknowledge also the importance of weather conditions mainly during germination and seedling establishment as the most sensible time of a plant life for the species composition in grasslands (e.g. Marañon & Bartolome, 1989).

However, in the present study remarkable changes in vegetation structure after abandonment of grazing have been found both in upper, and much stronger, in lower slope zone (chapter 3). The changes were identified as one main factor for the change in species richness and composition, also due to changing water availability through changing evaporation with changing vegetation structure. Therefore, it can be assumed that grazing and slope, functioning as a synonym for water stress gradient in strong Mediterranean climate, may act similar as stress factors on vegetation and traits. That is in line with the findings from de Bello et al. (2005), who assumed that, amongst others, both grazing (or disturbance in general) and climate act both as filters on plant functional traits. They assumed that life-cycle and reproductive strategies can be considered as examples of adaptations to both climate and grazing.

Against the background of the influence of different managements on vegetation development, also the influence on shrub encroachment was studied. The increase in frequency and cover of *Cistus* spec. on the burnt and burnt and ploughed areas indicates the problems of shrub encroachment in these regions after fire. Shrubs from the *Cistus* genera, as typical fire followers (Calvo et al., 2005; Buhk & Hensen, 2006; Moretti et al., 2008), showed enhanced germination after heat and smoke in several experiments. Therefore, the increase of *Cistus* species on the burnt areas is not surprisingly. This contradicts the assumption from Trabaud (2002) that a burnt community re-establishes identically. Due to fire enhanced germination of some species, combined with high competitive communities, vegetation communities may change after a fire with a high resilience for persistence of these communities. However, in an experiment the effects of heat and smoke on germination of typical dehesa species (chapter 7) were tested. Here, three out of six nano-phanerophyte-species tested from the *Cistus* genera showed also high germination rates not only in the heat and heat and smoke treatments, but also in the control treatments. This was interpreted e.g. by Calvo et al. (2005, for *Cistus ladanifer*) or Moretti et al. (2008, for *Cistus salviifolius*) mentioning that germination may take place not only after fire, but also in otherwise disturbed habitats. These may ensure survival of these species in times of low fire frequencies. In contrast, in the present study germination from *Cistus* spec. on the ploughed and grazed areas without influence of fire was rare or even not existing. This may be caused by missing heat or smoke trigger on germination on the ploughed and grazed areas. However, also missing quantity of viable seeds due to low abundance of *Cistus* shrubs on permanently grazed areas may cause low abundance and frequency of new germination of *Cistus* spec.. As for the investigation of soil seed bank of the different areas (chapter 6) the trays with soil samples were set in a fenced area in the study site without further treatments in order to exclude uncertainties referring to germination temperature. However, the influence of viability of the seeds as well as influence of fire as a trigger of germination could not be identified.

5 Dispersal in space – endozoochorous seed dispersal of Mediterranean dehesa species through cattle and pigs

5.1 Abstract

In disturbed habitats with frequent extinction and re-establishment of plants, effective dispersal mechanisms in space and time are essential for the persistence of plant species. Additionally, seed dispersal in space gains more and more importance both in times of land use changes followed by an increasing fragmentation of habitats as well as within climate change. Effective dispersal mechanisms ensure to reach favourable micro-sites and colonisation of new habitats. Many plants are limited in long-distance seed dispersal. Therefore, long distance dispersal by herbivores is discussed as one of the key-factors for their long-term survival in frequently disturbed habitats.

Mediterranean vegetation, and hereby dehesa grassland, should be specially adapted to dispersal through herbivores due to the long history of grazing in these areas. Thus, in a Mediterranean type dehesa, endozoochorous seed dispersal by two livestock species, namely pigs and cattle, were investigated in this study. Accordingly, species and their number of seedlings emerged from dung were analysed. A broad range of species were dispersed through the dung of both livestock with partly high numbers of seedlings per species. The number of seedlings emerging from pig dung was one third lower than from cattle dung but with no significances using the paired t-test, species number was significant lower in pig dung than in cattle. Thus, less species germinated from pig dung, but with partly higher seedling numbers per species in average. In conclusion, a large proportion of species endozoochorously dispersed through both cattle and pigs was found in the present study. However, no pattern could be detected regarding the differences in endozoochorous dispersal capability of both livestock.

5.2 Introduction

Seed dispersal in space gains more and more attention both in times of land use changes followed by an increasing fragmentation of habitats as well as within climate change (e.g. Cain et al., 2000; Higgins et al., 2003; Herrera & García, 2010; Walck et al., 2011). Effective dispersal mechanisms ensure the achievement of favourable micro-sites and the colonisation of new habitats (Cain et al., 2000). Mainly in disturbed habitats, where extinction and re-establishment are frequent, effective dispersal mechanisms are essential for the persistence of species (Levassor et al., 1990; Gallego Fernández et al., 2004). If effective dispersal mechanisms represent an advantage, adaptation for the enhancement of dispersal in space and time can be expected for a wide range of species and habitats.

Herbivores have already been proven as effective dispersal vectors in different studies (e.g. Fischer et al., 1996; Pakeman et al., 2002; Cosyns & Hoffmann, 2005). Many authors pointed out the role of herbivores for (extreme) long distance dispersal (Fischer et al., 1996; Malo & Suárez, 1997; Poschlod et al., 1998; Manzano & Malo, 2006; Ramos et al., 2006). Endozoochorous seed dispersal was considered as one of the main factors for the spread of species in habitats (Janzen, 1983; Jones et al., 1991; Malo & Suárez, 1998; Mouissie et al., 2005; Ramos et al., 2006), taking into account the retention time e.g. for cattle of 2-3 days and the travelling distance of up to 14 km / day (Squires, 1981). In addition, the immigration of species in new habitats (Dinerstein, 1991; Gardener et al., 1993; Malo & Suárez, 1994, 1997; Campbell & Gibson, 2001) was partly attributed to endozoochorous seed dispersal. Endozoochorous seed dispersal not only increases the frequency of many species on pastures (Welch, 1985; Malo & Suárez, 1994), but also the number of germinable seeds as well as species richness and diversity of soil seed bank (Malo et al., 1995; Malo & Suárez, 1995 b, c, 1996). The success of endozoochorous seed dispersal is influenced by different factors: the scoring effect of the livestock (Díaz, 2000), the passage of the seed through the gut (Gardener et al., 1993), as well as time and distance covered from the livestock during the passage of the seed (Poschlod & WallisDeVries, 2002).

Mainly in semi-natural grasslands, being developed and adapted over centuries by grazing through big herbivores, evidence of adaptations to endozoochorous seed dispersal was found by several authors (Collins & Uno, 1985; Gardener et al., 1993; Malo & Suárez, 1998). Many studies were carried out regarding endozoochorous seed dispersal by different herbivores as well as in different ecosystems. Thus, endozoochorous seed dispersal by cattle in grasslands in Sweden (Dai, 2000) and, in tropical and subtropical pastures (Gardener et al., 1993), by sheep of Mediterranean shrublands (Manzano et al., 2005) and, of Cistaceae species in south-eastern Spain (Ramos et al., 2006) were studied. Also legumes in north-west Syria (Russi et al., 1992), sheep and rabbit in the UK (Pakeman et al., 2002), as well as several studies about red deer and fallow deer, partly in combination with other herbivores (Malo & Suárez, 1995 a; Malo & Suárez, 1998; Gill & Beardall, 2001; Mouissie et al. 2005) were carried out.

Pigs represent a common livestock in Mediterranean dehesa, traditionally ranging on huge pastures in often mixed herds with cattle, sheep and horses. However, no studies are known up to now about endozoochorous seed dispersal capacity in Mediterranean grass- and shrublands. Therefore, the question if seedling number and species spectra dispersed endo-zoochorously by the omnivorous pig is similar to those of cattle was addressed in the present study.

5.3 Material and Methods

5.3.1 Endozoochorous data

The field work was carried out on the Dehesa San Francisco, which is described in chapter 2. In order to consider the period with the highest seed offer of this vegetation type, dung from cattle and pigs was collected monthly in 2005 from March to June. On each collection date, ten dung pads were sampled. As a reference, the fresh weight of each pad was measured. For this, the dung pad was divided into two parts and both parts were weighed. One part was dried afterwards and weighed again. The other half was mixed with sterilised soil (1:1) and spread in a layer of one centimetre over three centimetres of sterilized soil in individual trays and watered regularly. Each tray was protected against seed input from outside with a water and air permeable gaze. As a control, a tray with sterile soil was disposed together with the trays which contained the dung samples. The samples were placed in a fenced area of the study site to ensure natural climatic conditions. In order to maximize germination, the trays were left outside for one and a half year (two vegetation periods) enabling the germination of the largest possible number of dormant seeds (Malo, 2000). The emerged seedlings were identified and removed from the trays.

Tab. 5.1: Pastures ranged by cattle and pigs during the investigation period from March to June 2005.

	March	**April**	**May**	**June**
pigs	pasture 1	pasture 2	pasture 2	pasture 2
cattle	pasture 1	pasture 3	pasture 3	pasture 3

During the sampling period, pigs and cattle grazed in total on three pastures of the studied farm, each of a size of about 150 hectares. Even if different vegetation types were found on the studied farm due to slope zone and exposure, the vegetation of the pastures are similar. The area of about 150 ha of each pasture homogenizes differing vegetation pattern on smaller scales. In March the dung pads from cattle and pigs were collected from the same pasture. This was not possible from April to June, where cattle and pigs grazed on different, but neighbouring areas (Tab. 5.1).

5.4 Results

In total, 970 seedlings from 86 species were endozoochorously dispersed by cattle and 212 seedlings from 30 species by pigs (Tab. 5.2). Whereas mean seedling number per kg dry dung weight was about 30% lower in pig dung than in cattle dung, the total species number was about 60% lower. Despite the differences, the paired t-tests did not identify significant differences in seedling numbers between the two herbivores. In contrast, species number differed significantly (Tab. 5.3).

Tab. 5.2: Average, max. and min. seedling number per dung pad extrapolated to one kg dried dung weight and species number summarized over all dung pads of cattle and pigs. In total, 40 dung samples for each livestock were incorporated in the analysis.

	mean seedling number per dung pad extrapolated to one kg dried dung	max. seedling number per dung pad extrapolated to one kg dried dung	min. seedling number per dung pad extrapolated to one kg dried dung	total dry dung weight (g)	total species number	total seedling number
cattle	310	1885	34	3286	86	1045
pigs	203	1333	0	2513	30	510

Tab. 5.3: Paired t-test of seedling number and species number emerged from dung from cattle and pigs. n = month (March to June) with average seedling and species number of 10 replicates per month, from the year 2005. Level of significance: *< 0.05.

	t	n	p
seedling number	0.897	4	0.436
species number	-3.666	4	0.035 *

As shown in Fig. 5.1, the monthly variation of seedlings emerged from dung was relatively high for both cattle and pigs. For both livestock species seedling number showed a peak, which occurred in March for the pigs and in March and April for cattle. Seedling number in March was even higher from pig dung than from cattle dung. In the following months, seedling number strongly decreased for both livestock species, with very low seedling numbers emerged from pig dung.

The number of species (Fig. 5.2) emerged from cattle dung decreased from approximately 60 in March to about 25 in June, whereas number of species emerged from pig dung stayed nearly constant with about 15 species over the four months of investigation.

The high numbers of seedlings in March from pig dung are related to relatively few species, being mainly *Conyza albida* as well as *Polycarpon tetraphyllum*, *Sonchus asper*, *Chaetonychia cymosa* and *Juncus bufonius* (Tab. 5.5). In contrast, the high number of seedlings emerged from cattle dung in April was mostly due to the species *Chamaemelum fuscatum.* Species with high seedling numbers were only dominant in one month and also for only one livestock species. However, the strong dominance of some species found in pig dung was not as obvious in cattle dung. Average seedling number per species was about twice as high in pig dung compared with cattle dung. Thus, less species germinated in pig dung, but with in average higher seedling numbers per species.

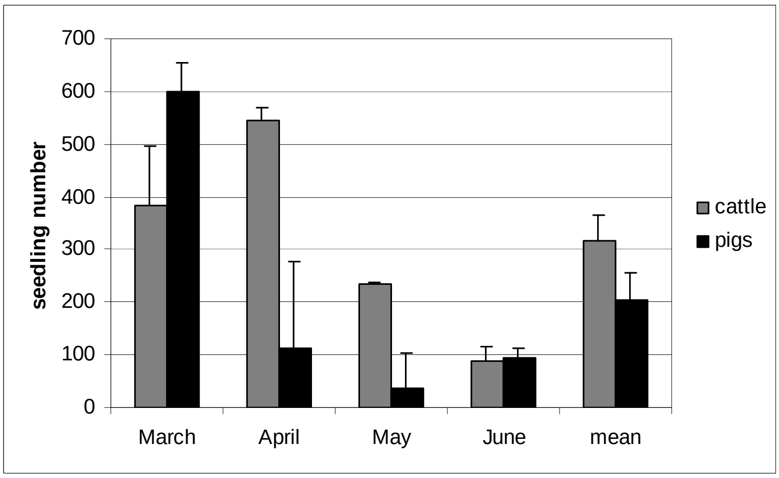

Fig. 5.1: Monthly average and total average over the four month of total seedling number emerged from cattle and pig dung from March to June (n=10) extrapolated to one kg. Indicated with error bars are the standard errors.

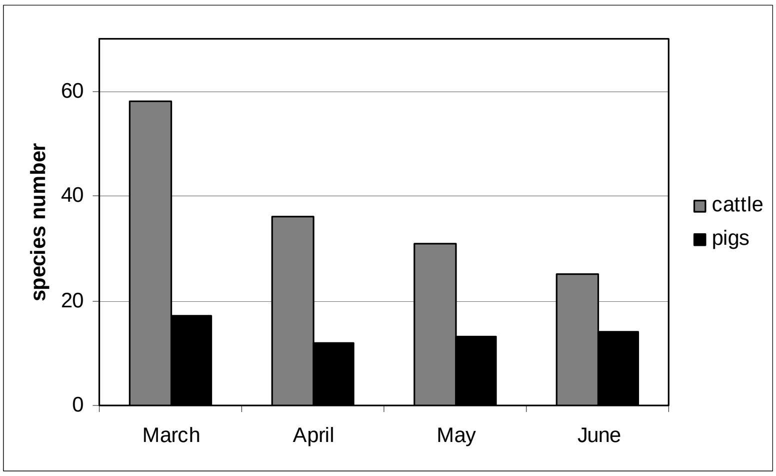

Fig. 5.2: Total monthly species number emerged from cattle and pig dung from March to June (n=10).

Tab. 5.4: a) Percentage of all species from cattle and pig pasture*, germinated both in cattle and in pig dung; b) Percentage of all species germinated from cattle respectively from pig dung and being sampled also on cattle and pig pasture*
*Incorporated are only plant species from vegetation samples from 2005 from the cattle and pig grazed pasture from upper and lower slope zone.

a)

percentage of all species from cattle and pig pasture distributed by	
cattle dung	pig dung
94%	34%

b)

Percentage of all species distributed by dung found also on cattle and pig pasture	
cattle dung	pig dung
59%	58%

About 94% of species from vegetation relevés from cattle and pig pasture germinated in cattle dung (Tab. 5.4), whereas the percentage of species from vegetation germinated from pig dung was with about 34% substantially lower. The percentage of all species germinated from both cattle and pig dung found also in vegetation relevés from cattle and pig pasture were for both herbivores with about 60% nearly equal.

Tab. 5.5: Species found in pig and cattle dung from March – June, sorted by their occurrence in pig and cattle dung. Shown are average seedling numbers / kg dry dung weigh per month. Number of dung pads per month and live-stock = 10.

		cattle					pigs				
		March	April	May	June	average	March	April	May	June	average
germinated only in cattle dung	*Chamaemelum fuscatum*	1,3	366,9	4,6		**93,2**					
	Plantago lagopus	2,2	2,2	37,3	2,5	**11,0**					
	Anagallis arvensis	35,1			1,4	**9,1**					
	Ranunculus tripartitus		32,7			**8,2**					
	Gastridium ventricosum	26,8		0,9		**6,9**					
	Tolpis barbata	18,7		0,9	0,9	**5,1**					
	Trifolium squamosum	10,4			5,7	**4,0**					
	Ornithopus compressus	5,7	4,1	0,9	1,1	**3,0**					
	Trifolium striatum	11,2				**2,8**					
	Lythrum acutangulum	8,4				**2,1**					
	Filago pyramidata	5,1			2,8	**2,0**					
	Geranium molle		6,7			**1,7**					
	Silene gallica	2,5		2,4	1,3	**1,6**					
	Malva sylvestris		6,1			**1,5**					
	Sherardia arvensis	5,2		0,9		**1,5**					
	Cistus salviifolius	4,4			0,9	**1,3**					
	Diplotaxis catholica	1,5	3,6			**1,3**					
	Hedypnois cretica	2,4	2,2			**1,1**					
	Trifolium stellatum			4,3		**1,1**					
	Lolium rigidum	1,5	2,5			**1,0**					
	Trifolium squarrosum	3,8				**0,9**					
	Trifolium tomentosum		1,9	1,8		**0,9**					
	Rumex bucephalophorus		1,9		1,4	**0,8**					
	Aira caryophyllea			3,1		**0,8**					
	Trifolium arvense	2,9				**0,7**					
	Ononis cintrana	1,5			1,2	**0,7**					
	Capsella bursa-pastoris		2,5			**0,6**					
	Anthyllis lotoides	1,3		1,2		**0,6**					
	Bromus diandrus		1,1	1,3		**0,6**					
	Biserrula pelecinus	1,3			1,0	**0,6**					
	Erodium botrys		1,9			**0,5**					
	Erodium moschatum		1,9			**0,5**					
	Stellaria pallida		1,9			**0,5**					
	Coronilla dura	1,8				**0,5**					
	Torilis nodosa	1,7				**0,4**					
	Bromus tectorum			1,6		**0,4**					
	Vulpia ciliata			1,6		**0,4**					
	Aphanes cornucopioides	1,5				**0,4**					
	Cistus crispus	1,5				**0,4**					
	Cynosurus cristatus	1,5				**0,4**					
	Sisymbrium officinale	1,5				**0,4**					
	Bromus hordeaceus		1,4			**0,3**					
	Erodium cicutarium	1,4				**0,3**					
	Euphorbia chamaesyce		1,4			**0,3**					
	Jasione montana	1,4				**0,3**					
	Pulicaria paludosa	1,3				**0,3**					
	Arabidopsis thaliana	1,3				**0,3**					
	Galium mollugo			1,2		**0,3**					
	Raphanus raphanistrum			1,2		**0,3**					
	Desmazeria rigida	1,1				**0,3**					
	Hypochaeris glabra	1,1				**0,3**					
	Leontodon longirrostris	1,1				**0,3**					
	Trifolium subterraneum	1,1				**0,3**					
	Illecebrum verticillatum	1,0				**0,3**					
	Misopates orontium	1,0				**0,3**					
	Papaver rhoeas	1,0				**0,3**					
	Sesamoides canescens	1,0				**0,3**					
	Crepis foetida	1,0				**0,2**					
	Psoralea bituminosa	1,0				**0,2**					
	Triticum turgidum				0,9	**0,2**					
	Briza minor			0,9		**0,2**					

Continuation of Tab. 5.5: Species found in pig and cattle dung from March – June, sorted by their occurrence in pig and cattle dung. Shown are average seedling numbers / kg dry dung weigh per month. Number of dung pads per month and livestock = 10.

		cattle					pigs				
		March	April	May	June	average	March	April	May	June	average
germinated both in pig and cattle dung	*Trifolium glomeratum*	92,4	4,0	4,0	8,4	**27,2**		3,7	0,9		**1,1**
	Trifolium cherleri	11,8	7,2	45,4	2,3	**16,6**	25,0	2,3		1,1	**7,1**
	Heliotropium europaeum	6,7		45,1	5,0	**14,2**	6,7			4,8	**2,9**
	Juncus bufonius	23,3	15,9	6,7	6,1	**13,0**	31,3	4,5	2,2	1,1	**9,8**
	Vulpia geniculata		13,3	21,4		**8,7**			0,5		**0,1**
	Cerastium glomeratum	8,8	10,2			**4,8**		2,1			**0,5**
	Erodium primulaceum		17,4			**4,4**		2,7			**0,7**
	Tuberaria guttata	9,3	1,1	7,0		**4,4**	16,7				**4,2**
	Conyza albida	7,2	1,3		8,9	**4,4**	137,7	22,4	19,1	30,2	**52,3**
	Polypogon maritimus	6,4	2,2	8,4		**4,3**	11,1				**2,8**
	Trifolium campestre	3,5	1,4	5,9	6,1	**4,2**	53,5		1,3	5,3	**15,0**
	Medicago polymorpha		1,1	3,7	8,2	**3,3**			0,5		**0,1**
	Chaetonychia cymosa		6,9		5,8	**3,2**	42,2	4,5	0,8	12,2	**14,9**
	Poa annua	9,5	2,8			**3,1**			0,8		**0,2**
	Plantago coronopus		6,9	4,0		**2,7**		3,7			**0,9**
	Sonchus asper	5,1	2,5	2,5		**2,5**	43,5	9,1	1,0	1,8	**13,8**
	Sonchus oleraceus	1,0		7,0	0,9	**2,2**	20,5	10,4	1,6	1,1	**8,4**
	Polycarpon tetraphyllum	1,0	5,3			**1,6**	50,0	33,9		2,2	**21,5**
	Spergularia rubra	1,3	1,9		1,4	**1,1**		2,2		2,2	**1,1**
	Chenopodium murale		1,1		2,2	**0,8**	6,3			4,0	**2,6**
	Paronychia echinulata	1,0			1,3	**0,6**				26,4	**6,6**
	Trifolium scabrum	1,1				**0,3**			1,0		**0,2**
	Melilotus elegans				0,9	**0,2**			1,0	0,7	**0,4**
	Gaudinia fragilis			0,9		**0,2**	12,5				**3,1**
germinated only in pig dung	*Senecio vulgaris*						29,1				**7,3**
	Lythrum portula						20				**5**
	Brachypodium distachyon						16,7				**4,2**
	Coleostephus myconis						16,7				**4,2**
	Euphorbia peplus								1,9		**0,5**
	Sonchus tenerrimus									1,8	**0,4**
	Number of species	16	18	13	13	86	13	12	12	13	24

5.5 Discussion

With in total 94 out of about 300, a large proportion of plant species of the local flora was dispersed through dung deposition in the present study. Other studies reported about a similar proportion of species of a local flora dispersed endozoochorously by herbivores, e.g. 107 out of about 350 species in cattle dung in a Mediterranean dehesa system (Malo & Suárez, 1995 c), 37 out of 57 species in rabbit pellets in a UK lowland dry grassland (Pakeman et al., 1998) and about 37 % of the species recorded in the vegetation were found in the dung of rabbit and sheep in the UK (Pakeman et al., 2002).

However, the number of seeds found in dung in the present study was comparatively small. For dry Mediterranean vegetation, large amounts of seeds were found in dung. E.g. Malo et al. (2000) found up to 3700 seeds / kg in cattle dung, 12400 seeds / kg in dung of red deer and 5000 seeds / kg in the dung of fallow deer. Azcárate et al. (2002) and Peco et al. (2005) argued that this vegetation type is adapted to dispersal through herbivores due to the long grazing history in these areas. The lack of morphological structures for dispersal from a high percentage of Mediterranean species compared to other, more humid vegetation types, are interpreted as a direct adaptation to endozoochorous seed dispersal. Also in temperate vegetation types, numbers of germinable seeds were higher. For instance, Stender et al. (1997) found at least 2500 seeds / kg cattle dung in Northwest German grasslands and Mouissie et al. (2005) determined 4604 seeds / kg cattle dung in Dutch heathlands. Other animals dispersed endozoochorously less striking numbers. 901 seeds / kg were found in pony dung and 1052 seeds / kg in sheep dung. The low numbers in this study may be caused by the low rainfall during the study period. Vegetation cover was about two third lower than in average years. Many species did not reach their flowering state before dying, and seed offer was extremely low for many species. Thus, also Malo & Suárez (1995 a) found in their study on a Mediterranean dehesa a strong correlation between viable seed numbers in herbivore dung and pasture phenology.

In the present study, average seedling number from pig dung was, with 203 seedlings / kg dry dung, one third less than from cattle dung with 318 seedlings / kg dry dung. Whereas no comparative studies about pigs are known from Mediterranean grasslands, Schönfelder (1998) compared pigs, cattle and horses in a contrasting habitat, namely in the wet floodplains of the Save in Croatia. Here, 2200 diaspores / kg germinated from cattle dung, and 380 diaspores / kg from pig dung. However, species number was with about 35 species similar for both herbivores. The small number of seeds in pig dung was confirmed by a study from Neugebauer (2004) about endozoochorous seed dispersal by pigs in wet and dry grasslands in Central Europe. He found 96 seeds / kg dung in the wet habitat and only 36 seeds / kg dung in the dry habitat. As in the present study pigs and cattle grazed on the same, respectively on neighbouring pastures, the same species composition was offered through pasture vegetation.

Although the differences between seedlings emerged from pig and cattle dung were not so high, pigs generally seem to disperse seeds from less species than cattle. One reason could be the different digestion system of the pig. Whereas cattle ruminates their fodder and therefore causes more mechanical damage to seeds, pigs have a more intense “chemical” digestion due to a longer digestion system with bigger capacity. This was approved by forage digestion experiments. The digestion was more complete through pigs (60%) than through horses (50-60%) and ruminants (50%; Bergner & Ketz, 1969). However, pigs ingest larger quantities of soil during their search and feed in contrast to other herbivores on sub-terrestrial biomass. These soil particles, especially the clay particles, could encase the seeds and protect them through the adsorption of aggressive digestion enzymes (Scheffer & Schachtschabel, 1992). This could help seeds of such a large proportion of species to survive the digestion system of pigs. However, with the intake of sub-terrestrial material the proportion of aboveground biomass decreases, and with this the likelihood of seeds being ingested. For example, Tucak (1996) found in studies about the content of wild boar stomachs a proportion of 23% of sub-terrestrial biomass. In another study, Briedermann (1986) showed a proportion of about 5% soil in the stomach content, which could occasionally rise up to 10%.

A high percentage of plant species mapped in vegetation relevés on cattle and pig pasture were also dispersed through cattle dung. This suggests a low selectivity of ingestion of plant species for cattle. In contrast, for pig dung values were considerably less. However, total number of species germinated in pig dung was also considerably less compared to cattle dung, which may explain the low number of species mapped on vegetation relevés and also germinated in pig dung. The nearly equal percentage of all species distributed by dung found also on cattle and pig pasture for both cattle dung and pig dung indicates also low selectivity for both livestock species regarding plant species. The low percentage for both species may be interpreted in regard to species richness due to different plant communities and patchiness with high species variability. As vegetation relevés were set in the non-shaded areas without bushes in southern slope in order to obtain high reproducibility, these vegetation relevés do not capture the species richness and variability beyond different plant communities.

The lack of any pattern regarding species composition suggests a negligible relevance of the digestion system of the herbivore cattle and the omnivore pigs. In the present study, these results are in accordance with the study from Mouissie et al. (2005), who explained the differences of endozoochorously dispersed seeds by cattle, sheep and pony with the more selective foraging behaviour and more restricted habitat use of sheep rather than with different gut survival capacities of the seeds. Hereby, they assumed that higher plant consumption should lead to higher seed ingestion. Furthermore, seed content in dung must also be seen in the context of seed offer through vegetation (Malo & Suárez, 1995 a; Mouissie et al., 2005; Bruun & Poschlod, 2006). Thus, the influence of the established vegetation on seed content of dung was shown in different studies (Malo & Suárez, 1995 b, 1995 c; Pakeman et al., 1999;

Neugebauer, 2004; Cosyns & Hoffmann, 2005). The high variation in seedling number emerged from dung between the months but also between the samplings and between single species detected in the present study reflects the patchiness of vegetation found in many other studies (for Mediterranean pastures: de Pablo et al., 1982; Lavorel et al., 1994). Due to topography, exposition, etc., different plant communities occurred in the study site in close vicinity. However, due to the huge areas each pasture covered, the entirety of plant communities was present at each pasture. Also the percentage of species from vegetation relevés from cattle and pig pasture germinated also from cattle and pig dung was with about 60% for both livestock low. This underlines the high diversity in species composition due to different location factors. As for the vegetation relevés comparable location factors were required, these only covering a small part of species variety.

Despite the low seedling number emerged from pig and cattle dung, about 30 % of all species found on the farm (herbaceous and shrubby species) were dispersed in cattle dung and about 10 % in pig dung. Due to the assumption, that not all species grown in the different habitats on the pastures were mapped, and due to the limited number of dung samplings in combination with a severe drought in the year of the experiment, the percentage of species potentially dispersed by dung may be much higher than in the present study. Despite this, the still high numbers of species dispersed through dung in the present study confirmed the assumption made by Bonn & Poschlod (1998) and also Neugebauer (2004), that in principle all diaspores could be dispersed by pigs. Therefore, pigs do not present a considerable filter for plant species, and both pigs and cattle must be considered as important dispersal vectors for Mediterranean dehesa vegetation in the present study.

6 Dispersal in time - Comparison of soil seed bank and differently managed pastures in a Mediterranean dehesa

6.1 Abstract

Dispersal in space and time is particularly important in highly disturbed habitats. Persistence in soil seed banks guarantees the re-colonization of disturbed sites as well as the plasticity of species in changing environments. Moreover, in Mediterranean grasslands with a predominance of annual species, soil seed bank plays a crucial role as a source for seedling recruitment. Therefore, a soil seed bank with a high percentage of persistent seeds has to be expected in ecosystems like the Mediterranean type dehesa with a high percentage of annual species in combination with a disturbance regime through farming. This should also be reflected in a high similarity between soil seed bank composition and vegetation.

To prove this, the soil seed bank from differently managed pastures from a Mediterranean type dehesa was analysed in the present study. For this, species number and seedling number per species in two soil depths, the upper soil layer 0-5 cm and the deeper soil layer 5-10 cm, were compared. In total, 76 species emerged from soil samples, with species number in the upper soil layer varying from 30 species from burnt pastures up to 42 species from cattle and pig pastures. The deeper soil layer had in general less species with 15 species from soil sampling from burnt pastures up to 26 species from soil samplings from pig pasture. In order to determine the similarity of soil seed bank composition and actual vegetation Sørensen’s similarity index was used. Similarity was generally low, with 23 % to 35 % for the upper soil layer and 17 % to 25 % for the deeper soil layer and the respective vegetation relevés. The ordination of soil samples and vegetation relevés reveals also differences between vegetation and soil seed bank samples.

Thus, even if a high number of species was found in soil seed bank, the expected similarity between vegetation and soil seed bank due to a severe disturbance regime and a predominance of annual species was not found in the present study.

6.2 Introduction

For annual species, which are depending on an annual germination, a survival of unfavourable years is only possible with a persistent seed bank (Thompson et al., 1996). A persistent seed bank un-couples population size from seed production of the previous vegetation period and provides every year germinable seeds (Figueroa & Davy, 1991; Rees, 1994). In highly disturbed habitats, in which annual reproduction is limited by disturbances, dispersal in space and time gains in importance (Levassor et al., 1990; Gallego Fernández et al., 2004). In habitats with changing environmental conditions, like the Mediterranean climate with high oscillations in precipitation over the years and within a year (Figueroa & Davy, 1991), dispersal in time plays a decisive role (Naveh, 1995), too. Under such conditions, soil seed bank guarantees the re-colonization of disturbed sites as well as the plasticity of species in changing environments (Thompson et al., 1996) due to the possibility of re-colonization from soil seed bank.

Similarity between actual vegetation composition and soil seed bank is therefore much higher in disturbed habitats with a predominance of annual species (Marañon & Bartolome, 1989; Levassor et al., 1990; Peco et al., 1998; Osem et al., 2006) than in perennial grasslands. Here, vegetative re-growth after disturbance dominates rather than germination from seeds (Milberg, 1993). Hence, the study of Levassor et al. (1990) about Mediterranean pastures showed a similarity (Sørensen's Similarity Index) of about 81% between species composition of soil seed bank and vegetation. Furthermore, the seed bank composition reflected both a successional stage as well as the intensity of disturbance. Highest species numbers are found at intermediate disturbance intensities with a drastic decrease at high intensities.

In Mediterranean dehesa vegetation with a long history of disturbance through agricultural use, a high similarity of species composition of vegetation and soil seed bank has to be expected. Furthermore, intensity of disturbance may produce patterns of species composition and seed density of soil seed bank of the respective areas as well as soil depth of the soil seed bank.

In the present study, vegetation from differently managed pastures from a Mediterranean dehesa have been compared with the respective soil seed banks, divided into two layers with different depths. As disturbance may have an influence on similarity of soil seed bank and vegetation, the different treatments should affect the soil seed bank differently. Therefore it should be reflected in the similarity index from the different pastures and the respective soil seed bank samples.

6.3 Material and Methods

6.3.1 Soil samples

In order to analyse the persistent soil seed bank alone, a quantification was carried out in February 2004 before the production of new seeds following the procedure of Peco et al. (2003). Differently managed pastures were chosen for the analysis (Tab. 6.1). With this, the influence of different disturbance factors on soil seed bank and hereby, the similarity of soil seed bank and actual vegetation has been investigated. Besides pastures grazed by pigs and mixed herds of cattle and pigs, also a burnt, with mixed herds of cattle and pigs grazed pasture, was sampled. Since habitat quality differed strongly at lower and upper slope, permanent plots were installed at both sites (0-15 % gradient and >15 % gradient) for cattle and pig pasture. All other areas were limited to a lower slope zone. The pig pasture was subdivided into a grassy pig pasture without shrubs, which was heavily disturbed by pigs through grazing and digging, and a pig pasture with shrubs (cover of shrubs >40 %). Due to the high cover of shrubs, it was only occasionally used by pigs.

Tab. 6.1: Number of soil samples per area and soil layer (0-5 cm and 5-10 cm).
Burnt: burned through a natural fire in summer 2003, grazed before and afterwards with cattle and pigs; cattle and pigs, lower slope: with cattle and pigs grazed pasture, situated in lower slope zone; cattle and pigs, upper slope: with cattle and pigs grazed pasture, situated in upper slope zone; pigs, shrubby: pig pasture with shrub cover >40 % ; pigs, without shrubs: pig pasture without shrubs;

area	soil layer	samplings
burnt	0-5 cm	10
	5-10 cm	9
cattle and pigs, lower slope	0-5 cm	10
	5-10 cm	10
cattle and pigs, upper slope	0-5 cm	10
pigs, shrubby	0-5 cm	9
pigs, without shrubs	0-5 cm	10
	5-10 cm	10

10 samples were randomly taken in 10 plots of 2x2 m² adjacent to the vegetation relevés. In areas with less than 10 vegetation sampling plots, the missing soil cores were taken in the direct neighbourhood of the other vegetation sampling plots.

Each cylindrical soil core (4 cm ø, depth 10 cm) was subdivided into two parts (0-5 cm and 5-10 cm), and the 10 sub-samples of each soil depth per plot were mixed in order to get one mixed soil sample per vegetation relevé and depth. Due to the stony soil and the directly imminent bedrock, only upper soil depth 0-5 cm could be sampled in both cattle and pig pasture, upper slope zone as well as in the shrubby pig pasture. The reduction of soil samples in some management types (Tab. 6.1) was caused by a disturbance through a fox, which was digging in the trays. These trays were excluded from the analysis.

In order to reduce the space needed for the cultivation of the soil, the seeds were concentrated and the small soil particles < 0.2 cm removed by washing the soil samples through a sieve. The remaining material was spread in 1 cm layer over 3 cm of sterilized soil in individual trays and watered regularly. Each tray was protected against seed input from outside with a water and air permeable gaze. As a control, a tray with sterile soil was disposed together with the concentrated soil samples (Ter Heerdt et al., 1996). All trays were set in a fenced area in the study site. With this, uncertainties referring to germination temperature and a possible necessity of breaking the dormancy of some species through temperature oscillations could be excluded. The seedlings were identified, counted and removed.

6.3.2 Vegetation samples

To compare species composition in the soil seed bank and the actual vegetation, only vegetation samples from the respective vegetation period 2004, in which soil samples were collected, were used. For more information about the method of vegetation samples see chapter 3.3.

6.3.3 Analysis

In order to compare species composition of soil seed bank samples and the respective vegetation relevés, Sørensen's Similarity Index was used following the formula from Mueller-Dombois & Ellenberg (1974):

$$QS = \frac{2a}{2a + b + c}$$

a: species number both common to seed bank and vegetation
b: species number exclusive to the vegetation
c: species number exclusive to the seed bank

Overall differences in species composition were analysed by means of multivariate statistics. A detrended component analysis (DCA) was used to analyse the similarity of vegetation and soil seed bank from different pastures. In a second step a subsequent correlation of species abundance with the axes was conducted. Ordination analysis was conducted with PC-Ord 4.33.

6.4 Results

In total 76 species emerged from 69 soil samples. From this, 70 species appeared in upper soil layers (0-5 cm) and 37 species in deeper soil layers (5-10 cm). In addition, the seedling number from deeper soil layers (5-10 cm) was about half the number from the upper soil layer (0-5 cm). Tab. 6.2 shows seedling numbers of species emerged from soil samples from the different areas and soil depths. Here, a high variability in the number of seedlings per species as well as in the number of seedlings in soil samples from the different pastures was found.

Compared to the upper soil layer (0 – 5 cm), fewer seedlings emerged from the deeper soil layer (5 – 10 cm) both in total as well as for most single species. Species like *Agrostis castellana*, *Coronilla dura*, *Filago lutescens*, *Illecebrum verticillata*, *Leontodon longirrostris*, *Plantago coronopus*, *Spergularia rubra* and *Tolpis barbata* grew from samples from upper soil layer in middle or high quantities, but were either not found at all or only in small frequencies in samples from deeper soil layer. *Biserrula pelecinus*, *Cistus crispus*, *Cistus ladanifer*, *Cistus salviifolius*, *Corrigiola littoralis*, *Euphorbia chamaesyce*, *Juncus bufonius*, *Lotus conimbricens*, *Trifolium arvense*, *Trifolium cherleri* and *Trifolium scabrum* had an even distribution between both soil depths. Furthermore, species like *Lythrum portula* had even higher seedling numbers in deeper soil layers compared to upper soil layers.

Finally, some species had high seedling numbers in the soil seed bank analysis but are less frequent in the actual vegetation in the respective areas, e.g. *Cistus ladanifer, Cistus salviifolius* or *Juncus bufonius.*

Tab. 6.3 shows species numbers from the soil seed bank and from the vegetation as well as the similarity of both on the basis of shared species and Sørensen’s similarity index. Through all pastures, the upper soil layer had a higher similarity with the actual vegetation regarding species composition than the deeper soil layer. For upper soil layer, the cattle and pig grazed lower slope zone had the highest similarity (Sørensen’s similarity index about 35 %) and the burnt as well as the cattle and pig grazed upper slope the lowest Sørensen’s similarity index (~ 23 %). For the deeper soil layer, Sørensen’s similarity index was lowest for the burnt area (17.5 %). The remaining two areas, the cattle and pig grazed, lower slope and pig pasture without shrubs, had indices of about 20.5 % and 25 %. Pig pasture without shrubs showed an almost similar Sørensen’s similarity index in the upper and lower soil layer.

Tab. 6.2: Number of seedlings emerged from soil samples from the different areas broken down into soil layer 0 - 5 cm and 5 - 10 cm. Burnt: burnt through a natural fire in summer 2003, grazed before and afterwards with cattle and pigs; cattle and pigs, ls: with cattle and pig grazed pasture, situated in lower slope zone; cattle and pigs, us: with cattle and pig grazed pasture, situated in upper slope zone; pigs, s: pig pasture with shrub cover >40 %; pigs, ws: pig pasture without shrubs

	seedling number								
	burnt, lower slope		cattle and pigs, upper slope	cattle and pigs, lower slope		pigs, without shrubs		pigs, shrubs	total seedling number
	0-5 cm	5-10 cm	0-5 cm	0-5 cm	5-10 cm	0-5 cm	5-10 cm	0-5 cm	
Agrostis castellana	**1**		**2**	**70**	**5**	**7**			**85**
Anagallis arvensis	**1**		**1**			**6**	**2**	**32**	**42**
Anthemis arvensis	**3**	**1**	**6**	**8**	**2**	**34**	**3**		**57**
Astragalus cymbicarpos	**1**								**1**
Barbarea intermedia							**1**		**1**
Biserrula pelecinus	**11**	**7**	**50**	**30**	**5**		**5**	**27**	**135**
Brassica barrelieri			**1**						**1**
Briza maxima									**0**
Carex spec.	**3**		**1**	**1**	**1**		**1**		**7**
Centaurium maritimum						**1**			**1**
Cerastium glomeratum		**1**		**1**		**3**			**5**
Chrysanthemum segetum				**1**		**4**			**5**
Cistus crispus						**4**	**1**	**39**	**44**
Cistus ladanifer	**24**	**58**				**62**	**54**	**96**	**294**
Cistus salviifolius	**55**	**38**			**3**	**9**	**6**	**241**	**352**
Cistus spec.								**15**	**15**
Coleostephus myconis	**3**	**1**	**1**			**4**			**9**
Coronilla dura	**15**	**1**	**4**	**2**		**1**	**1**	**44**	**68**
Corrigiola littoralis	**2**		**1**	**2**	**1**			**1**	**7**
Cuscuta planiflora	**5**							**3**	**8**
Diplotaxis catholica			**1**	**2**			**1**		**4**
Echium plantagineum					**1**				**1**
Erodium spec.	**1**			**2**					**3**
Erodium botrys				**2**	**1**				**3**
Erodium primulaceum				**1**					**1**
Euphorbia chamaesyce	**1**	**4**	**1**		**1**	**2**	**1**	**3**	**13**
Evax lusitanica			**3**			**13**	**1**	**1**	**18**
Filago lutescens	**17**		**10**	**12**		**29**		**7**	**75**
Gastridium ventricosum				**1**					**1**
Gaudinia fragilis						**2**			**2**
Geranium molle				**1**					**1**
Gymnostyles stolonifera	**26**			**10**	**1**				**37**
Heliotropium europaeum			**1**						**1**
Herniaria scabrida						**2**	**1**		**3**
Hypericum perforatum	**1**			**1**		**2**	**1**	**3**	**8**
Hypochaeris glabra			**1**						**1**
Illecebrum verticillata	**11**		**16**	**58**	**5**	**2**		**2**	**94**
Jasione montana								**1**	**1**
Juncus bufonius	**137**	**23**	**10**	**585**	**114**	**350**	**96**	**281**	**1596**
Lamarckia aurea			**1**	**1**	**1**				**3**
Leontodon longirrostris			**3**	**1**		**1**		**1**	**6**
Leontodon salzmannii									**0**
Lolium rigidum						**1**	**1**		**2**
Lotus conimbricens	**67**	**49**	**2**	**18**	**4**	**15**	**36**	**84**	**275**

Tab. 6.2 continued: Number of seedlings emerged from soil samples from the different areas broken down into soil layer 0 - 5 cm and 5 - 10 cm. Burnt: burnt through a natural fire in summer 2003, grazed before and afterwards with cattle and pigs; cattle and pigs, ls: with cattle and pig grazed pasture, situated in lower slope zone; cattle and pigs, us: with cattle and pig grazed pasture, situated in upper slope zone; pigs, s: pig pasture with shrub cover >40 %; pigs, ws: pig pasture without shrubs

	seedling number								
	burnt, lower slope		cattle and pigs, upper slope	cattle and pigs, lower slope		pigs, without shrubs		pigs, shrubs	total seedling number
	0-5 cm	5-10 cm	0-5 cm	0-5 cm	5-10 cm	0-5 cm	5-10 cm	0-5 cm	
Lupinus angustifolius									**0**
Lythrum portula					**7**	**1**	**1**	**1**	**10**
Misopates orontium			**2**	**1**	**1**	**1**		**1**	**6**
Ornithopus compressus				**1**					**1**
Ornithopus pinnatus								**2**	**2**
Paronychia argentea				**1**					**1**
Plantago bellardii	**1**			**1**					**2**
Plantago coronopus			**8**	**6**					**14**
Plantago lagopus				**51**					**51**
Plantago lanceolata			**28**	**16**	**2**	**1**			**47**
Poa annua				**1**					**1**
Raphanus raphanistrum						**1**			**1**
Rumex angiocarpus						**1**			**1**
Rumex bucephalophorus						**7**			**7**
Salvia verbenaca						**3**			**3**
Scorpiurus spec.	**1**		**2**	**1**		**1**		**14**	**19**
seedling	**39**	**10**	**41**	**37**	**7**	**24**	**12**	**175**	**473**
Silene gallica				**1**					**1**
Sisymbrium officinale						**1**			**1**
Sonchus tenerrimus				**1**					**1**
Spergularia rubra	**27**		**63**	**206**	**16**	**163**	**14**	**8**	**497**
Tolpis barbata	**2**					**14**		**2**	**18**
Trifolium spec.	**115**	**30**	**63**	**36**	**21**	**51**	**55**	**44**	**415**
Trifolium angustifolium									**0**
Trifolium arvense		**2**	**98**	**23**	**7**	**4**	**4**	**2**	**140**
Trifolium campestre	**13**								**13**
Trifolium cherleri	**1**		**19**	**9**	**13**	**7**	**9**	**1**	**59**
Trifolium scabrum		**1**	**2**	**4**	**8**	**4**	**10**	**17**	**46**
Trifolium subterraneum									**0**
Trifolium suffocatum				**1**	**2**				**3**
Tuberaria guttata	**1**			**10**			**1**	**3**	**15**
seedling number	**585**	**226**	**442**	**1217**	**229**	**838**	**318**	**1151**	**5006**
species number	**30**	**15**	**31**	**42**	**25**	**39**	**26**	**31**	**76**

Tab. 6.3: Number of species emerged from soil samples and mapped in the adjacent vegetation relevés. Total species number from both soil seed bank and vegetation relevés as well as number of shared species are given. Additionally, Sørensen's similarity index is given for each area and soil depth. Soil samplings are distinguished in upper and lower soil layer (0-5 cm and 5-10 cm). Burnt: burned through a natural fire in summer 2003, grazed before and afterwards with cattle and pigs; cattle and pigs, lower slope: with cattle and pig grazed pasture, situated in lower slope zone; cattle and pigs, upper slope: with cattle and pig grazed pasture, situated in upper slope zone; pigs, shrubby: pig pasture with shrub cover >40 %; pigs, without shrubs: pig pasture without shrubs

	soil depth	species number seed bank	species number vegetation relevés	species number total	shared species vegetation - seed bank	Sørensen's similarity index
burnt	0-5cm	30	65	84	11	23.2
	5-10cm	15		73	7	17.5
cattle and pigs, upper slope	0-5cm	31	61	81	11	23.9
cattle and pigs, lower slope	0-5cm	42	53	77	17	35.8
	5-10cm	25		69	8	20.5
pigs, without shrubs	0-5cm	39	78	101	15	25.6
	5-10cm	26		90	13	25.0
pigs, shrubby	0-5cm	32	73	87	17	32.4

The ordination from soil seed bank samples and the respective vegetation relevés (Fig. 6.1 for soil layer 0 – 5 cm and Fig. 6.2 for soil layer 5 - 10 cm) shows the differences in species composition and abundance between aboveground vegetation and soil seed bank. Within the group of vegetation plots as well as within the group of soil seed bank samples, a sub-grouping from the differently managed pastures can be seen. Three species, *Juncus bufonius*, *Lotus conimbricens* and *Spergularia rubra* were correlated to the soil seed bank samples from soil layer 0-5 cm and the four species *Leontodon longirrostris*, *Ornithopus compressus*, *Trifolium cherleri* and *Tolpis barbata* were correlated to the vegetation samples (Fig. 6.1).

For the soil layer 5-10 cm and the respective vegetation samples no species are correlated with soil seed bank, whereas eleven species are correlated to the vegetation samples: *Agrostis castellana*, *Anthemis arvensis*, *Eryngium campestre*, *Leontodon longirrostris*, *Lolium rigidum*, *Gaudinia fragilis*, *Ornithopus compressus*, *Plantago lagopus*, *Rumex angiocarpus*, *Tolpis barbata* and *Vulpia geniculata* (Fig. 6.2).

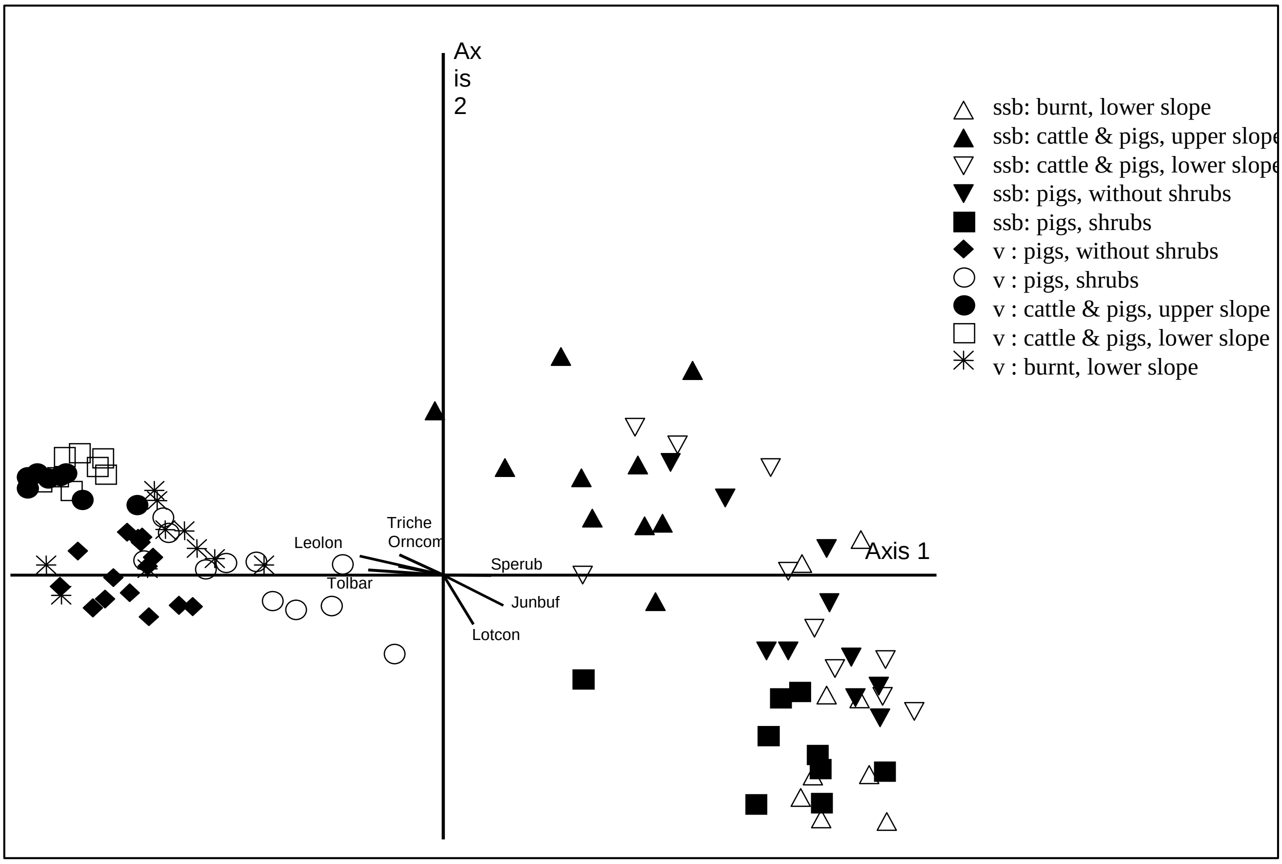

Fig. 6.1: DCA ordination of the vegetation of differently managed pastures and the respective soil seed bank samples from soil layer 0-5 cm. r²-cut-off-value > 0.25. ssb: soil seed bank samples; v: vegetation samples. Abbreviations of species names: Junbuf: *Juncus bufonius*, Leolon: *Leontodon longirrostris*, Lotcon: *Lotus conimbricens*, Orncom: *Ornithopus compressus*, Sperub: *Spergularia rubra*, Tolbar: *Tolpis barbata*, Triche: *Trifolium cherleri*. Axis 1 explains 41.1 % of variance, axis 2 explains 3.9 % of variance (Relative Euclidian distance).

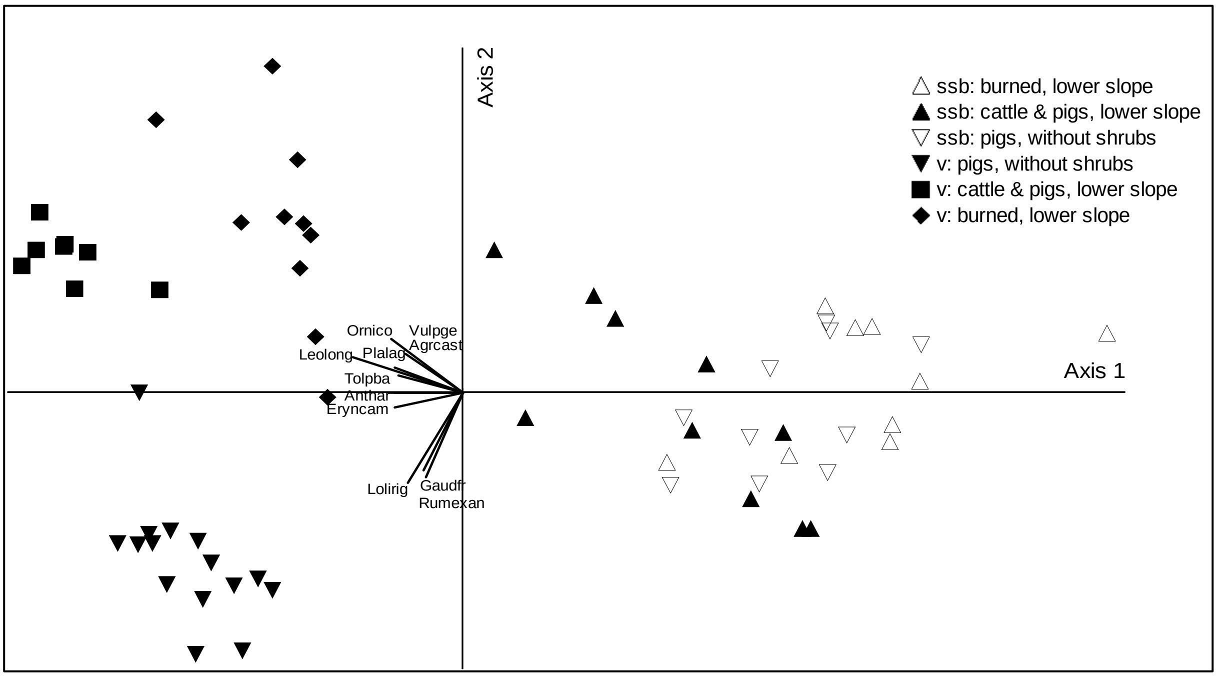

Fig. 6.2: DCA ordination of the vegetation of differently managed pastures and the respective soil seed bank samples from soil layer 5-10 cm. r^2-cut-off-value = 0.3. ssb: soil seed bank samples; v: vegetation samples. Abbreviations of species names: Agrcas: *Agrostis castellana*, Antarv: *Anthemis arvensis*, Erycam: *Eryngium campestre*, Gaufra: *Gaudinia fragilis*, Leolon: *Leontodon longirrostris*, Lolrig: *Lolium rigidum*, Orncom: *Ornithopus compressus*, Plalag: *Plantago lagopus*, Rumang: *Rumex angiocarpus*, Tolbar: *Tolpis barbata*, Vulgen: *Vulpia geniculata*. Axis 1 explains 49.8 % of variance, axis 2 explains 14.8 % of variance (Relative Euclidian distance).

6.5 Discussion

In general, the similarity between actual vegetation and species composition of soil seed bank was low in the present study. This is in contrast with the results from Peco et al. (1998), who found in their study high similarities between Mediterranean pasture vegetation and soil seed bank. However, Levassor et al. (1990) found, also for Mediterranean pastures, high similarities between vegetation and soil seed bank, but a generally low correspondence for recently ploughed and intensely disturbed plots. Furthermore, on the highly disturbed plots species number drastically decreased and floristic similarity was low. The much higher species number in the actual vegetation than in soil seed bank in recently ploughed sites was interpreted as an emptying of soil seed bank in the first year after ploughing, leaving behind the fraction of dormant seeds. This is in line with the findings in the present study, which showed lower similarities between vegetation and soil seed bank with increasing disturbance intensities (Fig. 6.3). If only the results from the upper soil layer (0 – 5 cm) are considered, two groups being different regarding their similarity with the respective vegetation can be identified.

The cattle and pig pasture in lower slope zone as well as the pig pasture with shrubs, having both a relatively high Sørensen’s similarity index of about 35 %, can be interpreted as one group. Both pastures had relatively low intensities of soil disturbances compared to the other pastures incorporated in the present study. On the areas, which were grazed with mixed herds of cattle and pigs, pigs had, considering the whole year, only a small influence on the vegetation. This can be explained through their limited activity radius and their in total small number. During the hot period, their activity radius was limited around their feeding place and water holes. In winter, the pigs ranged the pasture in groups in search for fodder. However, due to the small proportion of pigs in the mixed herds, their influence on vegetation was low. Although cattle comprises small disturbances through trampling, their main influence on vegetation is due to the partly removal of the above ground biomass. On the pig pasture with a much higher number of ranging pigs, their influence on soil due to digging was much stronger. However, pig pasture was divided in a grassy and a shrubby pasture. The high cover of shrubs on this part of the pig pasture prevents stronger soil disturbances in this area as the pigs avoid the bushy areas to the advantage of the more grassy areas of the pasture.

The second group identified consists of the burnt pasture, the pig pasture without shrubs and the pasture grazed with mixed herds of cattle and pigs in upper slope zone having all a Sørensen’s similarity index of about 25 %. Both burning as well as pig grazing in higher densities signifies an increase in disturbance of vegetation as well as soil. Disturbances, like grazing, burning and ploughing, generate opportunities for recruitment from the soil seed bank, which are giving advantage to species with persistent seed bank (Davies & Waite, 1998). Therefore, either directly after a severe disturbance like fire or in permanently disturbed pastures like pig pastures, a decline of soil seed bank through increased germination was assumed. The cattle and pig pasture from upper slope zone was not exposed to severe disturbance intensities in the last years. However, vegetation composition changes from year to year even under the same pasture management in a Mediterranean dehesa. Several studies found that species composition is strongly influenced by climate, and especially variation in rainfall during germination season in Mediterranean ecosystems (Marañon & Bartolome, 1989; Peco, 1989; Figueroa & Davy, 1991; Clary, 2008). Exposition and inclination amplify the effect of temperature and precipitation and cause therefore a stronger effect on vegetation. Therewith, natural oscillations of precipitation and related to this changing species composition in Mediterranean grasslands may be stronger pronounced in upper, south-facing slope. This may explain the lower conformity compared to cattle and pig pasture in lower slope zone.

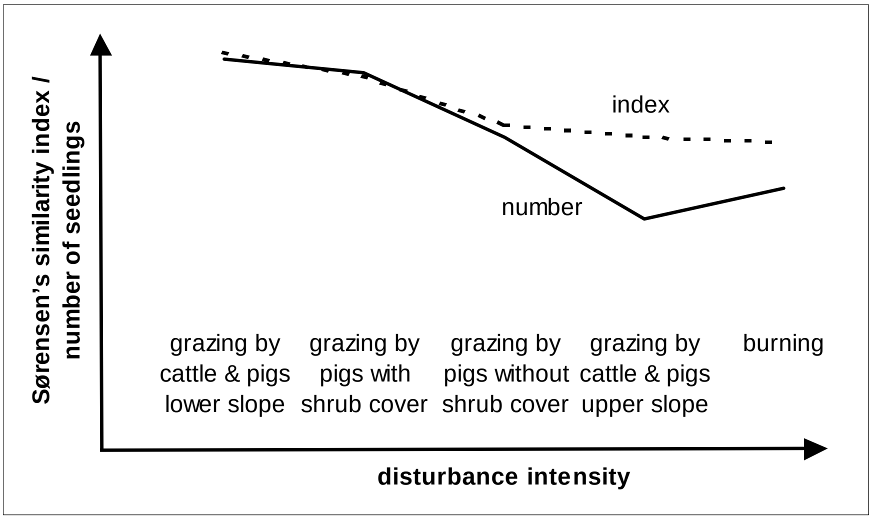

Fig. 6.3: Sørensen's similarity index of soil seed bank (layer 0-5cm) and actual vegetation and disturbance intensity due to the treatments of the pastures included in the present study.

Sørensen's similarity index matches with number of seedlings emerged from soil seed bank (for upper soil layer 0-5cm) for all five pastures, with low Sørensen's similarity index coincide with low seedling numbers and high Sørensen's similarity index coincide with high seedling numbers (Fig. 6.3). These results may support the hypothesis of emptying the soil seed bank after disturbances.

Beside the relatively low conformity between species composition of soil seed bank and the respective vegetation, both soil seed bank as well as vegetation showed high similarities within each pasture. As already discussed for the cattle and pig pasture from upper slope zone, the influence of precipitation with strong oscillations within and between years effects strongly species composition from one year to another (Figueroa & Davy, 1991). Due to a high percentage of species with persistent seed bank, Mediterranean vegetation is flexible and species re-establish again in favourable years (Thompson et al., 1996). These fluctuations in species composition in vegetation over the years have been exemplary shown for the cattle and pig grazed pasture in Fig. 3.3. Beneath disturbances in terms of pasturing and burning, the changes in species composition due to fluctuating precipitation may be reflected in the generally low similarity between soil seed bank and vegetation.

Altogether, a high number of seedlings as well as species were found in soil seed bank from different pastures exposed to different treatments. However, the expected high similarity between vegetation and soil seed bank as a function of disturbance intensity was not found in the present study.

7 Germination ecology of selected dehesa species

7.1 Abstract

The dehesa is one of the typical man-made habitats of the Mediterranean region. It has been developed through multiple land use types such as grazing and cork production. In addition, fire is considered to be another management tool responsible for the development of the dehesa.

Fire is known as a filter of the germination niche. Hereby, temperature and smoke are being responsible for the increase of the germination rate of many species. Regarding this, the hypothesis that fire played a key role in the development of the dehesa has been tested in the present work. For this, the germination behaviour of 27 typical dehesa species including shrubs and herbs has been investigated on heat and smoke sensitivity.

From the analysis, the 27 species can be categorized in four groups based on their germination behaviour after heat-shock and / or smoke primer-applications. Nine species showed increased germination rates after heat shock (e.g. *Cistus ladanifer, Psoralea bituminosa)* and four species after smoke application (e.g. *Diplotaxis catholica, Sesamoides caniscens)*. However, eight species showed indifferent germination rates throughout the treatments (e.g. *Hedypnois cretica, Lavendula stoechas)* and six species had too low germination rates in order to identify any adaptation (e.g. *Trifolium cherleri, Tuberaria guttata)*. Based on the analysis, species tested in this experiment showed a wide inter specific variation in their response to heat and smoke treatments.

As a result, the high proportion of species sensitive on heat and smoke supports the hypothesis that fire was an important factor in the development of the dehesa.

7.2 Introduction

The dehesa is one of the characteristic man-made ecosystems in the Mediterranean region, especially on the Iberian Peninsula. Its origin dates back to medieval times (Plieninger et al., 2003), originating from the “Bosque mediterráneo” through selective cutting of trees, leaving a wooded pasture with scattered trees of evergreen and deciduous oaks. Through the permanent production of arable crops, grazing by Iberian pig, sheep and cattle, cutting of firewood and cork, a multi-productive ecosystem (agro-silvopastoral use) with an extensive character has been developed and preserved over centuries up to present days (Olea & Viguera, 1999).

Up to now, many studies exist about the influence of fire on habitats and their plant species, demonstrating the influence of fire on vegetation all over the world (Arianoutsou & Margaris, 1981; Thanos & Georghiou, 1988; Keeley, 1991; Roy & Sonié, 1992; Valbuena et al., 1992; Crosti et al., 2006; Bylebyl, 2007). Many ecosystems have to be considered as fire prone or fire adapted. In seasonal dry grasslands, grazing and fire are considered as the major factors structuring these communities (Noy-Meir, 1995). The use of fire to facilitate hunting and food gathering is already known for the palaeolithic people in the Mediterranean. Since then, millennia of severe pressure due to burning, cutting and grazing non-arable lands, and clearing, terracing, and cultivating arable areas, have created a vast array of strongly human-modified landscapes (Pausas, 2006). Especially in Mediterranean type ecosystems, fire has therefore a strong influence on establishing and maintaining of plant communities (Naveh, 1975; Purdie, 1977; Trabaud & Lepart, 1980; Arianoutsou & Margaris, 1982). Thus, Trabaud (1994) gives a review of investigations from different authors about the influence of fire on the vegetation of the Mediterranean Basin in particular. It was concluded that the vegetation of the Mediterranean Basin is adapted even to frequent fire. Furthermore, Trabaud (1994) concluded that the present vegetation of the Mediterranean Basin results from many years of evolution during which plants acquired mechanisms to overcome the effects of fire as well as climatic (especially summer drought) factors.

Species may be adapted to fire by many ways: either to resprout from subterranean buds, by releasing seeds only after fire or through germination enhanced by heat and smoke. Several studies already investigated the effects of fire on the germination of a wide range of species from various habitats (e.g. van Staden et al., 2000; Baskin & Baskin, 2001; Keeley et al., 2005; Crosti et al., 2006). Heat-shock stimulated germination is widespread in many plant families and is found in many ecosystems (Christensen & Muller, 1975; Arianoutsou & Margaris, 1982; Kelly et al., 1992), also for Mediterranean Basin species (Herranz et al., 1998; Paula & Pausas, 2008). Whereas many studies found positive effects (Herranz et al., 1998; Keeley, 1998; Tieu et al., 1999; Gashaw & Michelsen, 2002; Pérez-Fernández & Rodríguez-Echeverría, 2003; Crosti et al., 2006), other studies showed no effect (Torres et al., 2006) or even negative effects of fire on germination (Valbuena et al., 2001). However, not only heat, but also smoke may trigger germination (Adkins et al., 2000; Enright & Kintrup, 2001; Adkins et al., 2004; Bylebyl, 2007). For Mediterranean Basin flora previous studies had so far found a limited response to smoke or charred wood (Pérez-Fernández & Rodríguez-Echeverría, 2003; Buhk & Hensen, 2006). However, Moreira et al. (2010) suggested that smoke stimulated germination may play an important role in eight out of 30 woody species from the Mediterranean Basin.

Whereas the effect of fire was mainly studied under natural conditions (e.g. Odion & Davis, 2000; Auld & Denham, 2006), only few studies were carried out investigating the effect of fire on germination under controlled conditions (e.g. Keeley et al., 2005; Crosti et al., 2006; Torres et al., 2006; Bylebyl, 2007). However, during fire, temperature in soil differs strongly in space and time depending on wind intensity, micro-relief, presence of big stones and rocks, distribution of litter and standing biomass (Trabaud & Oustric, 1989). Taking into account these hardly predictable factors, the influence of fire on vegetation is difficult to be estimated under natural conditions. Furthermore, for the Mediterranean Basin vegetation, only few studies are known dealing with the effect of smoke on germination (Crosti et al., 2006). For the dehesa system, Díaz et al. (2003) acknowledge that fire as well as pasturing act as disturbances which are keeping the coexistence of species and life forms and are maintaining the high diversity of the dehesa systems. The influence of fire should therefore be reflected in species adaptation to fire cues.

As up to now only single species or species groups have been studied, a habitat specific study was accomplished. For this reason, a spectrum of herbaceous and woody species of the dehesa was chosen in order to test if there are any adaptations in germination ecology to fire. Based on the number of studies revealing fire triggered germination for a wide range of species, the hypothesis was formed that heat and smoke triggered germination can be found over a significant range of species typical for a Mediterranean dehesa.

7.3 Material and Methods

The field work was carried out on the Dehesa San Francisco, which is described in chapter 2.

7.3.1 Selection of plant species

Herbaceous species characteristic for the dry pastures were chosen as well as eight woody species typical for the shrub-layer of a dehesa. 27 species from 11 families were selected (Tab. 7.1).

Tab. 7.1: Scientific name, family membership and life form of the 27 species used for the germination experiment.

plant species	family	life form	plant species	family	life form
Anagallis arvensis	Primulaceae	therophyte	***Genista hirsuta***	Fabaceae	nano-phanerophyte
Anthyllis gerardii	Fabaceae	hemicryptophyte	***Hedypnois cretica***	Asteraceae	therophyte
Anthyllis lotoides	Fabaceae	therophyte	***Lavendula stoechas***	Lamiaceae	nano-phanerophyte
Asphodelus aestivus	Liliaceae	geophyte	***Leontodon longirrostris***	Asteraceae	therophyte
Bromus hordeaceus	Poaceae	therophyte	***Phlomis purpurea***	Lamiaceae	nano-phanerophyte
Cistus albidus	Cistaceae	nano-phanerophyte	***Plantago coronopus***	Plantaginaceae	therophyte
Cistus crispus	Cistaceae	nano-phanerophyte	***Plantago lagopus***	Plantaginaceae	therophyte
Cistus ladanifer	Cistaceae	nano-phanerophyte	***Psoralea bituminosa***	Fabaceae	hemicryptophyte
Cistus monspeliensis	Cistaceae	nano-phanerophyte	***Pulicaria odora***	Asteraceae	geophyte
Cistus populifolius	Cistaceae	nano-phanerophyte	***Sesamoides canescens***	Resedaceae	hemicryptophyte
Cistus salviifolius	Cistaceae	nano-phanerophyte	***Silene gallica***	Caryophyllaceae	therophyte
Diplotaxis catholica	Brassicaceae	therophyte	***Trifolium cherleri***	Fabaceae	therophyte
Gastridium ventricosum	Poaceae	therophyte	***Trifolium tomentosum***	Fabaceae	therophyte
			Tuberaria guttata	Cistaceae	therophyte

7.3.2 Seed collection

Seeds were collected in spring / summer 2006 from ten individuals per species. The seeds were air-dried at room temperature and stored afterwards in a cooling chamber at 5° C.

7.3.3 Germination experiment

The effect of heat and smoke on germination was studied using heat-shock, smoke primer application, a combination of both, and two control treatments (Tab. 7.2). In total, five treatments were applied to 25 seeds respectively of each species, with eight replicates per treatment. Heat-application was applied without soaking the seeds in water previously. As the smoke-primer has to be prepared in water, the respective control “wet” consists of soaking the seeds in water for 24°h.

Tab. 7.2: Treatments applied to 27 species from Mediterranean dehesa vegetation. For the simulation of fire on germination, heat, smoke primer and both together were used.
W= 24 hours soaked in water; H = heat 10 min., 80°C; SP = 24 hours soaked in water with smoke primer

treatment number	treatment			treatment description
	W	H	SP	
1	-	-	-	control, dry
2	+	-	-	control, wet
3	-	+	-	heat
4	+	-	+	smoke
5	+	+	+	heat & smoke

The heat shock treatment was applied at a constant temperature of 80° C for 10 min. For the heat & smoke-primer treatment, the seeds were put into water prepared with smoke-primer for 24 h directly after the heat treatment. The smoke-primer was composed of absorbent paper, impregnated with a smoke solution from burnt celluloses leaded through distilled water. This dehydrated smoke-primer papers are available in packet form. 50 ml water had to be added to one paper in order to prepare a solution, in which the seeds are soaked for 24 h (Brown & van Staden, 1997).

Directly after the different treatments, the seeds were stored in the germination chamber at 16/8 °C and 14/10 h day-night rhythm and were watered as necessary. In the beginning, germination of the seeds was controlled every 2-3 days. With decreasing germination rate the control was reduced to once a week.

7.3.4 Data analysis

The effect of the different treatments on seed germination was studied by the analysis of average cumulative percentage of germination of the eight replicates per treatment and species. For significant differences in total germination rate between control and treatments within species, the pair-wise U-test was used.

7.4 Results

7.4.1 Classification in four groups based on germination response

Based on the results from the Man-Whitney-U-test (Tab. 7.13) it was possible to extract four groups:

A species with enhanced germination rate due to heat,

B species with enhanced germination rate due to smoke,

C species with no enhancement of germination rate in any of the treatments (indifferent group),

D species with too low germination rate for any classification.

Group A: heat triggered germination

Germination rate of 9 out of 27 species increased significantly after heat-shock treatment (Fig. 7.1): *Cistus albidus*, *Cistus crispus*, *Cistus ladanifer*, *Cistus monspeliensis*, *Cistus populifolius*, *Cistus salviifolius*, *Genista hirsuta*, *Psoralea bituminosa* and *Silene gallica*.

Whereas *Genista hirsuta* had an strong increase only in the heat treatment, all other species in this group showed a highly significant difference between both heat and heat & smoke treatments and the respective control groups.

Tab. 7.3: Germination rate (%) of the selected species in the different treatments and significant differences from Man-Whitney-U-Test (performed with SPSS 12.0) from germination rate of control, dry and heat treatment, control, wet and smoke treatment as well as control, wet and smoke & heat treatment. Classification based on significances between both control groups and the respective treatments.
Level of significance: *< 0.05.; **<0.005

	total germination rate					control, dry - heat		control, wet - smoke		control, wet - heat & smoke		classification
	control, dry	heat	control, wet	smoke	heat & smoke	U	p	U	p	U	p	
Cistus albidus	2.3 ± 0.37	16.3 ± 0.73	2.4 ± 0.94	1.8 ± 0.45	15.5 ± 0.68	0.0	**< 0.000**	31.0	0.959	0.0	**< 0.000**	heat
Cistus crispus	11.6 ± 1.18	21.6 ± 0.71	10.3 ± 0.77	9.6 ± 1.99	23.3 ± 0.88	0.0	**< 0.000**	31.0	0.959	0.0	**< 0.000**	heat
Cistus ladanifer	9.0 ± 1.21	21.3 ± 1.47	8.5 ± 0.80	6.8 ± 1.36	23.0 ± 0.53	2.0	**< 0.000**	22.0	0.328	0.0	**< 0.000**	heat
Cistus monspeliensis	4.4 ± 0.46	10.8 ± 0.53	3.5 ± 0.63	3.5 ± 0.78	8.3 ± 0.84	0.0	**< 0.000**	28.0	0.721	3.5	**0.001**	heat
Cistus populifolius	1.0 ± 0.46	20.9 ± 0.90	1.3 ± 0.45	1.8 ± 0.49	20.1 ± 0.83	0.0	**< 0.000**	24.0	0.442	0.0	**< 0.000**	heat
Cistus salviifolius	2.3 ± 0.49	17.3 ± 0.86	0.9 ± 0.30	1.6 ± 0.38	13.5 ± 1.50	0.0	**< 0.000**	19.0	0.195	0.0	**< 0.000**	heat
Genista hirsuta	4.0 ± 1.31	37.5 ± 4.21	2.5 ± 0.73	2.5 ± 0.73	6.0 ± 1.07	0.0	**< 0.000**	32.0	1.000	12.5	**0.038**	heat
Psoralea bituminosa	0.8 ± 0.37	14.0 ± 1.04	0.9 ± 0.23	0.5 ± 0.19	17.0 ± 0.80	0.0	**< 0.000**	22.0	0.328	0.0	**< 0.000**	heat
Silene gallica	13.9 ± 0.67	18.0 ± 0.65	11.3 ± 0.84	12.8 ± 2.00	19.0 ± 1.02	3.0	**0.001**	16.0	0.105	0.0	**< 0.000**	heat
Anagallis arvensis	7.6 ± 1.05	11.9 ± 1.22	12.3 ± 1.08	14.6 ± 2.20	17.1 ± 1.77	10.0	**0.021**	12.5	**0.038**	14.0	0.065	smoke
Diplotaxis catholica	7.1 ± 0.58	7.4 ± 0.84	8.3 ± 1.03	15.6 ± 2.37	12.4 ± 3.42	29.5	0.798	8.5	**0.010**	24.0	0.442	smoke
Plantago lagopus	14.3 ± 1.00	14.1 ± 0.90	11.5 ± 0.93	16.5 ± 2.44	18.5 ± 0.96	30.5	0.878	8.5	**0.010**	2.0	**< 0.000**	smoke
Sesamoides canescens	3.6 ± 1.12	0.5 ± 0.19	5.0 ± 0.50	13.6 ± 2.05	14.8 ± 1.11	8.0	**0.010**	8.0	**0.010**	0.0	**< 0.000**	smoke
Asphodelus aestivus	16.5 ± 1.30	11.8 ± 1.71	13.8 ± 0.88	10.4 ± 1.77	13.5 ± 1.15	11.5	**0.028**	18.0	0.161	28.0	0.721	indiff.
Bromus hordeaceus	24.6 ± 0.26	22.9 ± 0.58	24.5 ± 0.27	21.6 ± 3.09	23.4 ± 1.12	9.5	**0.015**	29.0	0.798	16.5	0.105	indiff.
Hedypnois cretica	19.1 ± 0.77	17.4 ± 0.82	18.5 ± 0.82	15.3 ± 2.23	19.3 ± 0.98	16.5	0.105	19.5	0.195	26.5	0.574	indiff.
Lavendula stoechas	21.4 ± 0.73	20.5 ± 0.65	20.5 ± 0.68	16.8 ± 3.68	22.3 ± 0.56	22.0	0.328	28.0	0.721	15.0	0.083	indiff.
Leontodon longirrostris	20.5 ± 1.34	20.8 ± 0.77	20.1 ± 1.25	18.4 ± 2.67	20.5 ± 0.68	30.5	0.878	31.5	0.959	29.5	0.798	indiff.
Phlomis purpurea	18.3 ± 0.37	14.6 ± 1.05	18.6 ± 0.89	18.8 ± 2.70	18.8 ± 1.06	3.5	**0.001**	14.0	0.065	31.0	0.959	indiff.
Plantago coronopus	22.3 ± 0.67	22.3 ± 0.84	21.6 ± 0.56	18.8 ± 2.73	23.0 ± 0.53	30.5	0.878	25.5	0.505	17.5	0.130	indiff.
Pulicaria odora	19.6 ± 0.71	18.8 ± 0.70	17.9 ± 1.08	16.1 ± 2.88	18.1 ± 0.35	23.5	0.382	30.5	0.878	30.5	0.878	indiff.
Anthyllis gerardii	1.5 ± 0.33	1.8 ± 0.41	2.0 ± 0.19	2.1 ± 0.44	1.9 ± 0.23	28.0	0.721	28.5	0.721	28.5	0.721	not poss.
Anthyllis lotoides	1.8 ± 0.31	3.8 ± 0.62	1.8 ± 0.45	1.4 ± 0.42	1.5 ± 0.42	10.0	**0.021**	26.5	0.574	28.0	0.721	not poss.
Gastridium ventricosum	0.3 ± 0.16	0.5 ± 0.27	0.5 ± 0.19	1.1 ± 0.48	1.3 ± 0.50	27.0	0.645	26.0	0.574	22.5	0.328	not poss.
Trifolium cherleri	0.9 ± 0.30	0.9 ± 0.30	1.6 ± 0.32	1.1 ± 0.23	1.0 ± 0.33	32.0	1.000	20.5	0.234	20.5	0.234	not poss.
Trifolium tomentosum	1.4 ± 0.46	1.4 ± 0.26	1.6 ± 0.46	1.5 ± 0.38	1.0 ± 0.46	30.0	0.878	31.5	0.959	21.0	0.278	not poss.
Tuberaria guttata	1.5 ± 0.46	1.0 ± 0.33	2.0 ± 0.42	2.0 ± 0.46	1.9 ± 0.58	25.5	0.505	31.5	0.959	28.5	0.721	not poss.

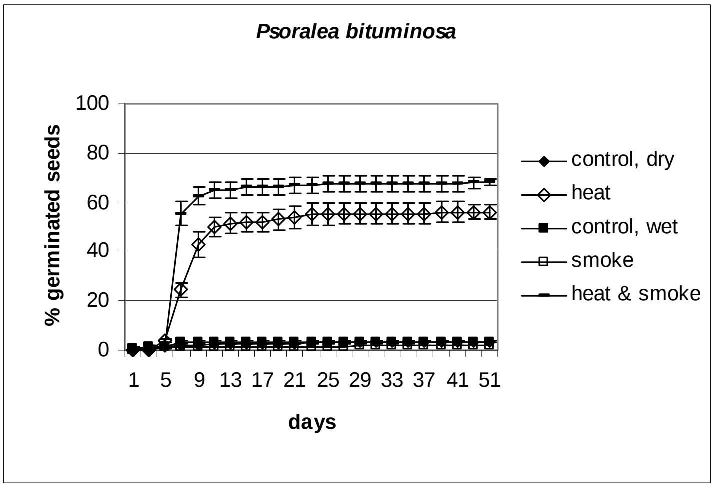

Fig. 7.1: Group A: Cumulative number of germinated seeds for *Psoralea bituminosa*, exemplary for the nine species categorized in the group with enhanced germination after heat and heat & smoke treatment (see also Appendices Fig. A-1 to Fig. A-3). For description of treatments see Tab. 7.2.

Group B: smoke triggered germination

Four species out of 27 had enhanced germination rate due to smoke with enhanced germination rate in the smoke treatment as well as in the smoke and the heat & smoke treatment, but not in the heat treatment alone (Fig. 7.2): *Anagallis arvensis*, *Diplotaxis catholica*, *Plantago lagopus* and *Sesamoides canescens*. All four species showed also a relatively high germination rate in both controls. Whereas *Anagallis arvensis*, *Plantago lagopus* and *Sesamoides canescens* showed nearly the same enhancement in germination rate for both the smoke treatment and the heat & smoke treatment, solely *Diplotaxis catholica* had a higher germination rate in the smoke treatment than in the heat & smoke treatment.

Group C: indifferent germination rate

Eight species, *Asphodelus aestivus*, *Bromus hordeaceus*, *Hedypnois cretica*, *Lavandula stoechas*, *Leontodon longirrostris*, *Phlomis purpurea*, *Plantago coronopus* and *Pulicaria odora*, showed no differences in germination between the different treatments and both controls (Fig. 7.3). Two of these species, *Bromus hordeaceus* and *Phlomis purpurea*, showed a delay in germination in the heat and the heat & smoke treatment with significant differences between control, dry and the heat treatment. Until the end of the experiment, this delay diminished for both species.

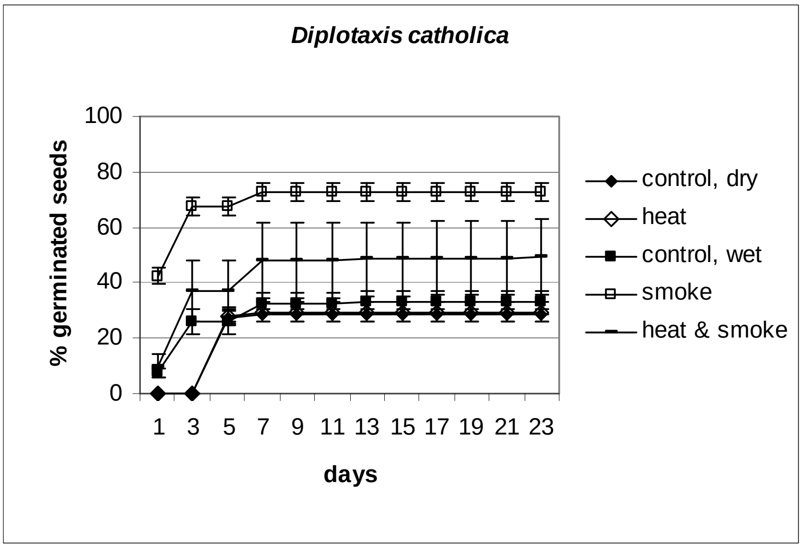

Fig. 7.2: Group B: Cumulative number of germinated seeds for *Diplotaxis catholica*, exemplary for the group of four species with enhanced germination after smoke and smoke & heat application (see also Appendices Fig. A-4). For description of treatments see Tab. 7.2.

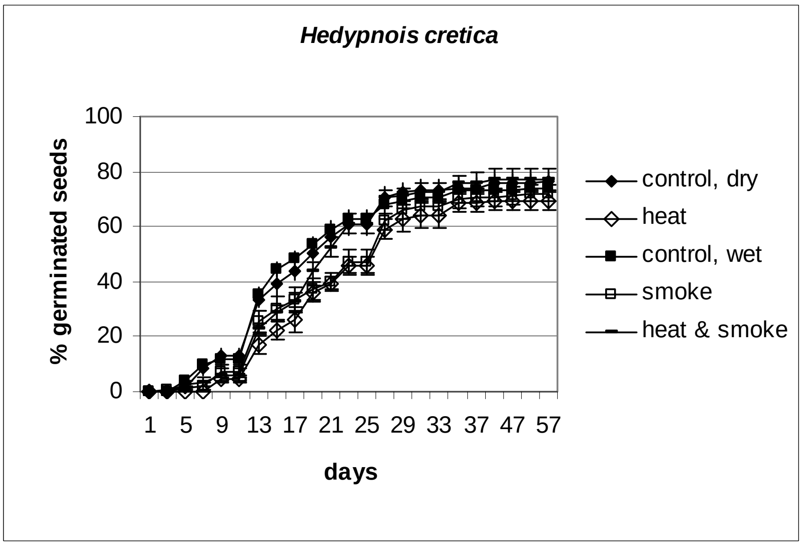

Fig. 7.3: Group C: Cumulative number of germinated seeds for *Hedypnois cretica*, exemplary for the group of eight species without any difference in germination between control and applications (see also Appendices Fig. A-5 to Fig. A-6). For description of treatments see Tab. 7.2.

Group D: species with too low germination rate

Six species (*Anthyllis gerardii*, *Anthyllis lotoides*, *Gastridium ventricosum*, *Trifolium cherleri*, *Trifolium tomentosum*, *Tuberaria guttata*) were excluded from the analysis due to a too low germination rate (see Appendices Fig. A-7 to A-8).

7.4.2 Cross-group trends in germination

From the species with heat and heat & smoke triggered germination classified in group A, four species (*Cistus crispus*, *Cistus ladanifer*, *Cistus monspeliensis* and *Silene gallica*) had also enhanced germination rates in the control treatments as well as in the smoke treatment. For all four species, germination of control and smoke treatment was about half of the germination rates after the heat and heat & smoke treatment (Fig. 7.4).

One species categorized in group B, *Sesamoides canescens* and three species categorized in group C, *Asphodelus aestivus*, *Bromus hordeaceus* and *Phlomis purpurea* had a significant lower germination rate in the heat treatment compared with control, dry (Fig. 7.5).

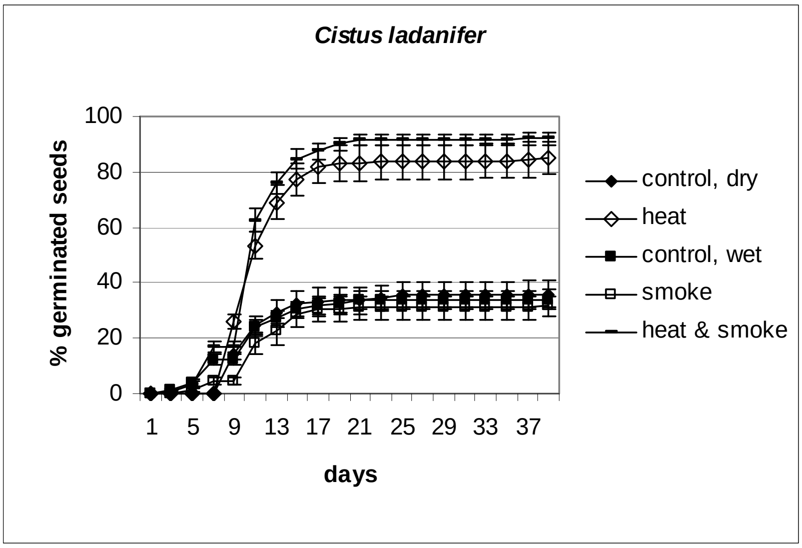

Fig. 7.4: Cumulative number of germinated seeds for *Cistus ladanifer* (exemplary for the species with enhanced germination after heat and heat & smoke treatment, but with also high germination rates in the smoke treatment and the control, wet treatments). For description of treatments see Tab. 7.2.

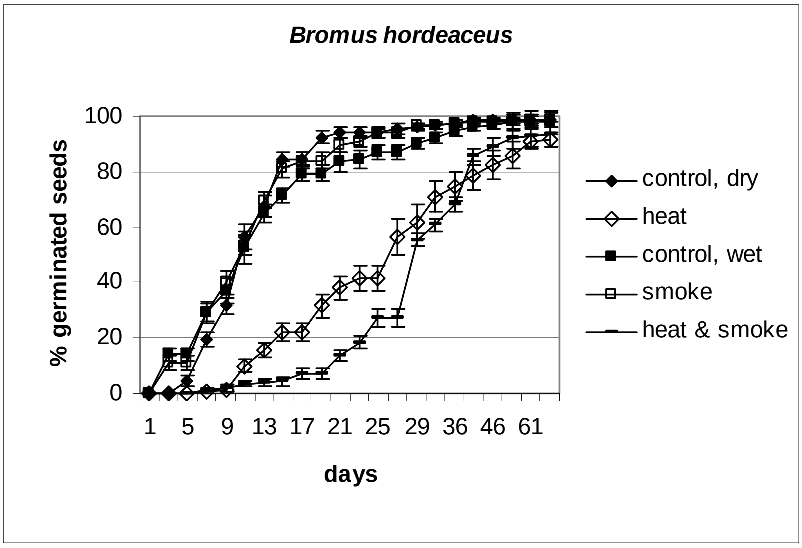

Fig. 7.5: Cumulative number of germinated seeds for *Bromus hordeaceus* (exemplary for the species with a delay in germination in the heat and heat & smoke treatment). For description of treatments see Tab. 7.2.

7.5 Discussion

Enhanced germination rate after heat-shock and / or smoke treatment was found in 14 out of 27 species from Mediterranean dehesa vegetation tested in this experiment. Heat triggered germination, with high germination rates in the heat and heat & smoke treatments but hardly any germination in both controls was found for five species from the group with heat triggered germination. These five species consist of three Cistaceae (*Cistus salviifolius*, *Cistus populifolius* and *Cistus albidus*) and two Fabaceae (*Genista hirsuta* and *Psoralea bituminosa*). Seeds of hard-seeded species, e.g. Cistaceae and Fabaceae in the Mediterranean Basin, tend to withstand in several studies very high temperatures and their germination was stimulated by heat (Herranz et al., 1998, 1999; Valbuena et al., 2001; de Luis et al., 2006; Moreira et al., 2010). Heat may favor germination through the loss of dormancy, especially in seeds with impermeable seed coats (Baskin & Baskin, 2001; Black et al., 2006).

However, the remaining species categorized in the group with heat triggered germination, three Cistaceae species, *Cistus ladanifer*, *Cistus crispus* and *Cistus monspeliensis*, one Fabaceae *Anthyllis lotoides* and also the Caryophyllaceae *Silene gallica,* showed high germination rates in the heat and heat & smoke treatments, but also – in lower numbers – germination in both control treatments. These findings support the results from Calvo et al. (2005) for *Cistus ladanifer* that germination may take place not only after fire, but also in otherwise disturbed habitats, ensuring the survival of the species in times of low fire frequencies. Also Moretti et al. (2008, for *Cistus salviifolius*) and Cruz et al. (2003, for *Erica australis)* considered enhanced germination as an adaptation to unpredictable disturbances and environmental constraints rather than an adaptation to repeated burning. Herranz et al. (1998) found in their study about the influence of heat on seed germination of seven Mediterranean species from Fabaceae although a fraction (6-27%) of soft-coated seeds which germinates in the control without any pre-treatment. This fraction enables the maintenance of populations during periods without fire and explains the colonizing ability in disturbed areas, like abandoned fields or vegetation gaps, without fire. This is also in line with findings from Buhk & Hensen (2006), who found low abundance of “fire seeders” for south-eastern Spain together with a successful regeneration of these species in otherwise disturbed sites. Buhk & Hensen (2006) explained their findings historically with strong human disturbances in combination with low fire frequencies as the fuel load is limited due to the dry conditions in the Mediterranean Basin.

The four species classified in the present study in the group with smoke triggered germination belonged to four different families. This is in line with findings from the study of Enright & Kintrup (2001) concerning fire triggered germination of heath-woodland in Australia as well as Crosti et al. (2006) for nine phanerophytes and one geophyte from the Mediterranean Basin. It was shown that dry heat was a specific requirement for hard-seeded species (e.g.

Fabaceae), whereas smoke was the most effective trigger for species from a broad range of other families. In addition Moreira et al. (2010) suggested for eight out of 21 woody species that smoke is playing an important role in germination and growth of these Mediterranean Basin species. Smoke leads to intense scarification of the seed surface (van Staden et al., 2000). For Mediterranean Basin flora, different studies suggested that smoke has a limited role as a post-fire germination cue (e.g. Buhk & Hensen, 2006, Reyes & Trabaud, 2009). However, the exact mechanism how smoke influences germination is not fully understood yet.

The lethal effect of heat, as found in many studies about different species and habitats (Roy & Sonié, 1992; Tarrega et al., 1992; Noy-Meir, 1995; Herranz et al., 1998; Habrouk et al., 1999; Valbuena et al., 2001) could only partly be shown in the present study. Whereas the delay in germination rate in the heat treatment of *Bromus hordeaceaus* and *Phlomis purpurea* nearly diminished until the end of the experiment, *Sesamoides canescens* and *Asphodelus aestivus* had a significant lower germination rate in the heat treatment compared with control, dry. This indicates a damaging of the seeds through heat in the experiment for these species.

In Mediterranean ecosystems with a long fire history, heat sensibility may be an important factor in the competition with other, fire adapted species. However, the lethal effect of heat on more of the species would probably be identified with higher temperatures than the limited temperature of 100°C used in this experiment. This assumption is approved by measurements in wildfires in different ecosystems (California chaparral: Odion & Davis, 2000; Mediterrane-an-type ecosystems of south-eastern Australia: Auld & O'Connell, 1991; Bradstock & Auld, 1995; for savannah-sites: Jensen et al., 2001), which showed a wide range in temperatures in the 0-5 cm deep soil layer with temperatures up to 150° C and very variable heat exposure periods depending on depth and fire intensity.

Altogether, species tested in this experiment showed a wide interspecific variation in their response to heat and smoke treatments. Using the results of this experiment as a basis of interpretation, the influence of the management tool fire as well as an increasing number of wildfires should have serious influences on species composition of dehesa grasslands. The influence of heat and smoke on single species as well as species composition have to be studied closely in order to evaluate the influence of fire as a management tool in different ecosystems.

8 Conclusions and perspectives

In the present study, the effect of change of grazing and management measures on species composition in a Mediterranean dehesa was analysed. Hereby, dispersal in space and time as well as the influence of fire on germination ecology of selected species were studied in order to get a better understanding of the mechanisms causing differences in species composition. From this it was seen that different grazing regimes and management measures had a clear effect on vegetation composition, species number and partly vegetation structure on the study site. It was also shown that seed dispersal is common both from soil seed bank as well as endozoochorously. A broad range of species germinated from soil seed bank and emerged from dung samples both from cattle and pigs. Furthermore, the enhancement of germination due to heat and smoke was shown for several species typical for the study site.

The present study gives a broad overview over the effect of change in management on vegetation in the special ecosystem dehesa. Up to today, such a comprehensive study was not carried out in this ecosystem. Besides a vegetation study, the factors which were expected to influence most species development and richness, being in this ecosystem dispersal and fire, were incorporated as well. For the substitution of traditional grazing systems, pig grazing could be recommended in the present study with respect to species numbers. However, the results suggested that in long term removal of aboveground biomass, which may not be sufficient with single pig grazing, may be the decisive factor for the preservation of species richness in this ecosystem. Therewith, in long term cattle grazing may be the factor preserving highest biodiversity and ecosystem functioning in the most effective way. Fire and ploughing, which are frequently used in open landscapes as substitutions for traditional farming practices, seem to change species composition in long term due to long lasting species as well as a change in location factors in dehesa ecosystem.

However, all managements discussed as subsidies, which were burning, ploughing and a combination of both, were accompanied by pasturing with cattle and pigs in the present study. Still it would have been desirable to include single managements like burning and ploughing without further grazing in order to represent better the substitution of traditional management systems as they are used today. Since subsidies are chosen on the basis of cost and time calculations, the combination of different managements are unlikely to be realized. The influence of the permanent grazing regime may partly overlay the effect of the subsidies on vegetation, especially in long term. The force of adaptation of vegetation may be much stronger under permanent grassing pressure than under single management measures. For example no relation could be shown in the present study between the enhanced germination rate of the species tested in laboratory experiments to heat and smoke and their development in abundance and frequency on the burned pastures compared with the not burned pastures. This was also interpreted as a stronger need of adaptation to the permanent grazing pressure than to single fire events. Fire in low frequency and intensity may have similar effects on vegetation than grazing pressure. E.g. Belsky (1992) found only few effects of fire on the cover of individual species. A low temperature fire may therefore only reduce aboveground biomass, functioning simply as a duplicated effect of intense grazing. However, if succession takes place due to abandonment, management measures like burning or ploughing with total removal of the aboveground biomass may present a much stronger interference on vegetation. Furthermore, with increasing amount of biomass, typical for succession after abandonment, fire intensity may increase. Moreno & Oechel (1994) found in their study about chaparral in California fire intensity as a crucial factor in controlling post-fire dynamics. Therewith, depending on vegetation structure on the study site, different effects of single managements on vegetation without further pasturing have to be expected.

Even though the study showed a clear effect of the different grazing regimes and management measures on vegetation composition, species number and partly vegetation structure, the prediction of the long-term development of the vegetation after a change in the management system was not possible within the present study. The results of the analysis of change in species composition following the change in grazing and management measures suggest that the effect on vegetation represent rather long-term changes over a longer period than four years. For predictions concerning the long-term development of the study site, management and monitoring need to be continued so that general rules can be revealed.

In order to find effective conservation measures, processes like climate change and fragmentation of the landscape has to be considered as well (e.g. Opdam & Wascher, 2004). These both may represent the biggest challenges in the coming years regarding the preservation of Mediterranean old landscapes. For the Mediterranean Basin, a pronounced decrease in precipitation, especially in the warm season, together with a pronounced warming is projected by Giorgi and Lionello (2007), reviewing climate change projections over the Mediterranean region. For the Mediterranean dehesa, which is called the last border for separating the Mediterranean countries from the desert (Amaro, 1988), the intensifying of the Mediterranean climate may signify an extinction of this ecosystem. Opdam & Wascher (2004) concluded in their study that under a changing climate two strategies for survival of species in a fragmented landscape may be found: local adaptations and spatial extensions to appropriate habitats. E.g. Landsberg et al. (1999), and also McIntyre et al. (1999) found modifications of species reaction to drought through grazing and management systems, which would imply an impact of management on the ability for local adaptation of plant species to changing climatic conditions.

The results of the present study are indicating also strong interactions between vegetation development due to different grazing regimes, management measures and precipitation in the respective vegetation period. The reaction of species composition and species number of the differently managed areas after the dry year 2005 together with the differing water capacity of the areas indicates an interaction of management and climate on species composition. Subsequently, the question raise whether the adaptability of species to the expected climate change with predicted increase in temperature and drought in summer may be influenced by the managements of Mediterranean ecosystems. If management influences the adaptiveness of the Mediterranean species to changing climate, an adapted management may play a decisive factor for the survival of these ecosystems on a longer perspective. Therewith, studies are necessary which filter out the effect of weather fluctuations and management in order to understand better the overlaying or even themselves intensifying effects. Such studies may help to conclude the influence of management measures on the adaptiveness of species to the expected climate change. Besides local adaptation to changing climate, the expansion of range towards shifting habitats is also discussed by Opdam & Wascher (2004). However, intact dispersal vectors are essential for the expansion of range of plant species and communities. Increasing fragmentation of the landscape may reduce the resilience of plant communities in their habitat as well as the depression of re-colonisation of sites due to limited dispersal vectors (Opdam & Wascher, 2004; Chust et al., 2006). Thus, the present study reveals the potential influence of dispersal on vegetation in the ecosystem dehesa with a broad range of species germinated both from soil seed bank and also from cattle and pig dung. However, no general pattern was found for habitat specific conclusions about their influence on dehesa vegetation. For instance, neither the relationship of vegetation of the differently managed areas and endozoochorous seed dispersal by cattle and pigs was found, nor the influence of seed functional traits on endozoochorous dispersal capacity of the different species. Therewith, the present study gives a broad overview about the potential importance of dispersal for Mediterranean species of a dehesa, however, more studies are needed in order to filter out the importance of single dispersal mechanisms for the conservation of this ecosystem. Since efficient dispersal mechanisms may be decisive both in changing environments as well as with increasing fragmentation for the resilience of plant communities as well as for the migration of species in new habitats, studies are needed in order to get generalisable functional results. Based on this, conservation measures should be implemented which support and restore the most effective dispersal mechanisms.

Following this, the present study presents an important approach taking up the set of difficulties about the substitution of traditional managements on the vegetation in old, cultural landscapes, which are adapted to a mostly century long grazing tradition. It shows fundamental results, which should, in order to identify the mechanisms behind these vegetation developments, be intensified in studies about the single aspects of the present study.

9 Summary

The Mediterranean dehesas are an example of an agro-ecosystem with very high biodiversity. The management regimes of the Spanish and Portuguese dehesas are complex due to their traditional, multi-factorial use by different livestock, extensive agricultural exploitation as well as production of firewood and cork over many centuries. The formerly huge areas covered with a dehesa type ecosystem in Mediterranean Spain are nowadays reduced to about 3 – 3.5 Mio. ha. However, the decline of open, semi-natural grasslands like the Spanish dehesas as well as their typical and species-rich flora and fauna is caused both by abandonment and agricultural intensification and represents a global problem. Habitats and thereby species adapted to diverse management regimes, which are differing in scale, frequency and intensity, are difficult to preserve. Manifold factors are influencing vegetation development in these environments.

A special role in the pasturing system of a dehesa plays the Iberian pig, which roam traditionally free on large pastures in herds mixed with cattle. Besides their grazing activities, pigs have due to their digging in the soil a special impact on vegetation. With the disruption of the normally dense vegetation cover, the digging increases patchiness and vegetation dynamics. Therewith, in the present work, the effect of cattle and pig grazing and abandonment of use on the vegetation of a Mediterranean dehesa was studied. The experimental set-up represents a gradient regarding both the removal of aboveground biomass and soil disturbances. The effects of other traditional managements on vegetation were also incorporated in the present study. Here, burning, ploughing and a combination of both, often being used as subsidies in order to keep abandoned agricultural sites open, were studied. In the Mediterranean dehesa, most of the common, late-successional species (e.g. *Cistus* spec., *Lavandula* spec., *Genista* spec.) possess physical or chemical defences against grazing. Periodic ploughing or occasional burning was traditionally used in order to control these undesired shrub vegetation on these grasslands. Therewith, besides the analysis of the herbaceous vegetation, the effects of different managements on species from the genera *Cistus* were investigated, too. To reveal the mechanisms behind the effect of management regimes on vegetation patterns and dynamics, dispersal in space and time of species as well as germination requirements of selected species of the respective vegetation types were also studied. First, endozoochorous dispersal for both cattle and pigs was analysed. Since resilience of plant species gains in importance with increasing disturbance intensity and frequency, the composition of soil seed bank from differently managed areas were investigated, too. Here, the investigation focused on the influence of management on soil seed bank composition and similarity of soil seed bank and actual vegetation. In case of Mediterranean vegetation, adaptation to fire, incorporated here as fire triggered germination and tested in a laboratory experiment, has to be regarded as well.

Therewith, the influence of fire on germination ecology on 27 typical species from Mediterranean dehesa grassland was investigated.

Chapter 1 gives a general introduction together with a short outline of the subjects of the respective chapters. Information about the ecosystem dehesa, its development, actual situation and threats are given. The dehesas in Spain and Portugal – descended from the Bosque mediterráneo, the Mediterranean hard leaves forest – are the result of a century long multi-factorial use by different livestock (cattle, sheep, goats and pigs), production of firewood and cork as well as extensive agriculture exploitation. Until now, herbivores are one of the driving factors for the development and maintenance of the Mediterranean Basin landscape and its adapted vegetation. Dehesa grassland includes some of the most species-rich communities outside the tropics and is being listed in the Flora-Fauna-Habitat-Directive. As most of the old, cultural landscapes, the Spanish dehesas are threatened through abandonment as well as intensification of farming.

In chapter 2, the study area and study site are described. Field work has taken place at the farm "Dehesa San Francisco", a well-preserved dehesa (open woodland with *Quercus ilex* and *Q. suber*) located 70 km north of Seville. The farm is run by the Fundación Monte Mediterráneo with ecological livestock breeding of pigs, cattle and sheep on 700 ha.

Chapter 3 focuses on the effect of changes in the traditional grazing system on vegetation. Therewith, in order to show the effect of different grazing regimes on vegetation, traditional pig grazing as a reference was compared to alternative management regimes such as cattle and pig grazing and to abandonment. These management regimes represent a disturbance gradient regarding both the removal of aboveground biomass and soil disturbances. To meet the requirements of the heterogeneous landscape, lower and upper slopes were analysed separately. The different management regimes resulted not only in different species numbers, but also in a specific plant composition. After four years, species number was highest on pig pasture, followed by the cattle and pig pasture, being lowest at the fallow. Furthermore, species turnover, which was chosen as an indicator for diversity, was higher on fallow site than on both pastures. The development of species composition was identified using a detrended correspondence analysis. Whereas species composition changed over time in the two grazing systems, the influence of slope remained clearly visible throughout the years.

Chapter 4 deals with the effects of traditional treatments (burning, ploughing and burning and ploughing) on species composition. Ploughing and, less frequently, burning are common management measures against shrub encroachment in grazed Mediterranean dehesas. Both, species composition as well as species number differed between the managed areas as well as between the managed areas and the solely grazed area. However, species numbers were similar again in the last study year for all areas. As species composition differed until the end of the project compared to the solely grazed areas, some kind of memory of the vegetation regarding disturbances was indicated through several persistent species. Based on the question if different managements as well as slope zone influences soil moisture and its effect on species composition, an analysis of soil moisture of the differently used areas was incorporated in the present study, too. Management has a strong influence on water capacity of soil as well as species composition and species number. Furthermore, the influence of management on shrub encroachment was studied. *Cistus* spec. as typical phryganic plants from the Mediterranean Basin showed an increase on the burned and burned and ploughed areas compared to the ploughed and solely grazed pastures, indicating the management problems of encroachment of these unwanted shrubs after fire hazards.

In disturbed habitats, where extinction and re-establishment are frequent, effective dispersal mechanisms in space and time are essential for the persistence of plant species. Additionally, seed dispersal in space gains more and more importance in times of land use changes followed by an increasing fragmentation of habitats as well as climate change. Mediterranean vegetation, and hereby dehesa grassland, should be especially adapted to dispersal through herbivores due to the long history of grazing in these areas. Accordingly, species and the number of seedlings emerging from cattle and pig dung were analysed in a endozoochorous seed dispersal study in chapter 5. A broad range of species was dispersed through the dung of both livestock with partly high numbers of seedlings per species. Whereas the number of seedlings emerged from pig dung was about 30 % lower than from cattle dung, without being significant using the paired t-test, species number was significantly lower in pig dung than in cattle. Thus, less species germinated from pig dung, but with partly higher seedling numbers per species in average. In conclusion, a large proportion of species endozoochorously dispersed through both cattle and pigs was found in the present study. Thus, both pigs and cattle must be considered as important dispersal vectors for Mediterranean dehesa vegetation. However, no pattern in respect of seed traits was detected regarding the differences in endozoochorous dispersal capability of both livestock.

Persistence in soil seed banks guarantees the re-colonization of disturbed sites. In Mediterranean grasslands with a pre-dominance of annual species, soil seed bank plays a crucial role as a source for seedling recruitment. Thus, chapter 6 deals with the soil seed bank from differently managed pastures from the study site. Species number and seedling number per species in two soil depths, the upper soil layer 0-5 cm and the deeper soil layer 5-10 cm, were compared. In total, 76 species emerged from soil samples, with species number in the upper soil layer varying from 30 species from burned pastures up to 42 species from cattle and pig pastures. The deeper soil layer had less species with 15 species from soil samplings from burned pastures up to 26 species from soil samplings from the pig pasture. Similarity of soil seed bank composition and actual vegetation was generally low, with 23 % to 35 % for the upper soil layer and 17 % to 25 % for the deeper soil layer and the respective vegetation relevés. Similarity decreased with increasing disturbance intensities. This can be interpreted as an emptying of soil seed bank after disturbances due to an increased germination rate from the soil seed bank, leaving behind the fraction of dormant seeds. Besides disturbances of soil and vegetation, also the fluctuating precipitation may be reflected in the generally low similarity between soil seed bank and vegetation. Strong oscillations of precipitation within and between years strongly effects germination and survival of seedlings and with it species composition from one year to another. These changes in species composition due to fluctuating precipitation may be reflected in the generally low similarity. Whereas the actual vegetation is strongly effected by the yearly precipitation, the persistent soil seed bank represents the range of species over the years. In addition, the ordination of soil samples and vegetation relevés revealed the differences between vegetation and soil seed bank samples. Thus, even if a high number of species was found in soil seed bank, the expected similarity between vegetation and soil seed bank due to a severe disturbance regime and a predominance of annual species was not found in the present study.

Besides grazing, fire is one of the major factors shaping Mediterranean type ecosystems. Also for the Mediterranean dehesas, fire is considered to be a management tool for their development. Fire is known as a filter of the germination niche, with temperature and smoke being responsible for the germination of many species. Taking this fact into account the effect of heat and smoke on the germination of 27 selected species has been tested in chapter 7. The 27 species were categorized in four groups based on their germination behaviour after heat-shock and / or smoke primer-applications. Nine species showed increased germination rates after heat shock (e.g. *Cistus ladanifer, Psoralea bituminosa)* and four species after smoke application (e.g. *Diplotaxis catholica, Sesamoides caniscens)*. However, eight species showed indifferent germination rates throughout the treatments (e.g. *Hedypnois cretica, Lavendula stoechas)* and six species had too low germination rates in order to identify any adaptation to heat and / or smoke (e.g. *Trifolium cherleri, Tuberaria guttata).* All six *Cistus*-species incorporated in the experiment showed enhanced germination rates, approving their classification as phryganic species. Altogether, species tested in this experiment showed a wide variation in their response to heat and smoke treatments. Using the results of this experiment as a basis for interpretation, the influence of the management tool fire as well as an increasing number of wildfires should have serious influences on species composition of dehesa grasslands.

In chapter 8, the results were discussed in the overall context of the study. Based on this study, subsequent demand of research was identified. For predictions concerning the long term development of sites, management and monitoring has to be continued so that general rules can be revealed. Furthermore, in order to find effective conservation measures, processes like climate change and fragmentation of the landscape have to be considered as well. In addition, if management influences the adaptiveness of Mediterranean species to changing climate, an adapted management may play a decisive factor for the survival of these ecosys-

tems on a longer perspective. As efficient dispersal mechanisms may be decisive both in changing environments as well as with increasing fragmentation, studies are needed in order to get generalisable functional results. Based on this, conservation measures should be implemented which support and restore these dispersal mechanisms

10 Zusammenfassung

Die Dehesa Spaniens ist ein Beispiel eines landwirtschaftlich genutzten mediterranen Ökosystems mit einer sehr hohen botanischen als auch zoologischen Diversität. Das Managementsystem einer Dehesa ist aufgrund ihrer jahrhundertealten, traditionell sylvo-agropastoralen Nutzung durch unterschiedliches Weidetier, extensiven Anbau von Nutzpflanzen sowie der Produktion von Feuerholz und Kork sehr komplex. Die ehemals großen Flächen, welche in Spanien mit Dehesa bedeckt waren, haben sich heutzutage auf 3-3,5 Mio. Hektar reduziert. Der Rückgang von offenen, semi-natürlichem Grasland und damit einhergehend der daran angepassten artenreichen Flora und Fauna stellt heutzutage ein globales Problem dar. Verursacht wird dies sowohl durch Nutzungsaufgabe als auch Nutzungsintensivierung. Da Störungen, welche in Art, Stärke und Häufigkeit schwanken, einen vielfältigen Einfluss auf die Vegetationsentwicklung haben, sind störungsgeprägte Lebensräume sowie die daran angepassten Arten schwierig zu erhalten.

Eine besondere Rolle spielt im Beweidungssystem der Dehesa das Iberische Schwein, welches traditionell in gemischten Herden mit Rindern auf großen Flächen frei weidet. Neben dem Abgrasen der oberirdischen Vegetation haben Schweine aufgrund ihrer ausgeprägten Wühltätigkeit zur Futtersuche einen besonderen Einfluss auf die Vegetation. Dadurch wird die ansonsten oft dichte Pflanzendecke unterbrochen und damit die Diversität an Mikrostandorten sowie die Vegetationsdynamik erhöht. Basierend darauf wurde in der vorliegenden Studie der Einfluss von Rinder- und Schweinebeweidung sowie Nutzungsaufgabe auf die Vegetation des Systems Dehesa untersucht. Dieses Untersuchungsdesign stellt einen Störungsgradienten sowohl bezüglich der oberirdischen Vegetation als auch des Bodens dar. Zusätzlich wurde der Einfluss der Managementmethoden Brennen, Pflügen und eine Kombination aus beiden auf die Artenzusammensetzung der Vegetation hin untersucht. Als Managementmethoden wurden solche ausgewählt, welche traditionell gegen die oft drohende Verbuschung der Weiden eingesetzt werden. Da die Arten der Dehesa, welche oft die Verbuschung einleiten (z.B. *Cistus* spec., *Lavendula* spec., *Genista* spec.), häufig einen physischen oder chemischen Fraßschutz besitzen, reicht alleinige Beweidung zur Offenhaltung der Weiden auf längere Sicht meist nicht aus. Aufgrund dessen wurde neben der Analyse der krautigen Vegetation ebenfalls typische, an Feuer angepasste Arten der Gattung *Cistus* untersucht. Die Analyse der Ausbreitung in Raum und Zeit wurde in die aktuelle Studie mit einbezogen, um die entscheidenden Faktoren bezüglich der Vegetationsentwicklung bei einer Änderung des Managements mit zu betrachten. Aufgrund dessen wurde das Potential der Samenausbreitung durch Endozoochorie für sowohl Rinder als auch Schweine analysiert. Da die Resilienz von Pflanzenarten in einem störungsgeprägten Habitat an Wichtigkeit gewinnt, wurde ebenfalls die Zusammensetzung der Samenbank auf den unterschiedlich beweideten und gemanagten Flächen analysiert. Eine langlebige Samenbank sowie eine erfolgreiche quantitative und qualitative Keimung hieraus erhöht die Resilienz der Arten und damit des Ökosystems nach Störungen. Hierbei lag der Fokus auf dem Einfluss des Managements auf die Zusammensetzung der Samenbank sowie der Ähnlichkeit der Samenbank und der aktuellen Vegetation. Da Feuer häufig als Pflegemaßnahme gegen Verbuschung genutzt wird sowie auch natürliche Feuer eine wichtige Rolle in der Entwicklung der Mediterranen Vegetation spielen, wurde die Anpassung von typischen Arten der Dehesa an Feuer mittels eines Laborexperiments untersucht. Hierbei wurde der Einfluss von Hitze und Rauch auf die Keimungsökologie von 27 Arten des Untersuchungsgebiets analysiert.

Kapitel 1 gibt eine generelle Einführung in das Thema sowie einen kurzen Abriss über die folgenden Kapitel. Es wird ein Überblick über das Ökosystem Dehesa, seine Entwicklung, aktuelle Situation und Gefährdungen gegeben. Die Dehesas in Spanien und Portugal – hervorgegangen aus dem Bosque mediterráneo, dem Mediterranen Hartlaubwald – ist das Ergebnis einer Jahrhunderte alten sylvo-agropastoralen Nutzung durch verschiedenes Nutzvieh (Rinder, Schafe, Ziegen und Schweine), der Produktion von Feuerholz und Kork sowie der extensiven ackerbaulichen Nutzung. Auch heutzutage ist Beweidung immer noch eine der treibenden Faktoren für die Entwicklung und den Erhalt der Landschaft des Mediterranen Beckens und ihrer daran angepassten Vegetation. Das Grasland einer Dehesa beinhaltet eine der artenreichsten Gemeinschaften außerhalb der Tropen und ist in der Flora-Fauna-Habitat-Richtlinie aufgeführt. Wie viele andere alte Kulturlandschaften auch ist die Spanische Dehesa durch Nutzungsaufgabe und Nutzungsintensivierung stark gefährdet.

In Kapitel 2 wird das Untersuchungsgebiet und die Versuchsflächen vorgestellt. Die Feldarbeit erfolgte auf der Farm „Dehesa San Francisco“, einer gut erhaltenen Dehesa bestehend aus mit *Quercus ilex* und *Q. suber* licht bewaldeten Weiden. Die Farm ist 70 km nördlich von Sevilla gelegen und wird von der Fundación Monte Mediterráneo bewirtschaftet. Die 700 ha große Fläche der Farm wird ökologisch mit gemischten Herden aus Schweinen, Rindern und teilweise Schafen beweidet.

Kapitel 3 fokussiert auf den Einfluss der Änderung des traditionellen Beweidungssystems auf die Vegetation. Um den Einfluss unterschiedlicher Beweidungssysteme auf die Vegetation darzustellen wurden die alternativen Beweidungssystemen Rinder- und Schweinebeweidung in gemischten Herden sowie Brache mit der traditionellen Schweinebeweidung als Referenz verglichen. Mit diesem Untersuchungsdesign wurde ein Störungsgradient sowohl für die Störung der oberirdischen Vegetation als auch für die Störung des Bodens beschrieben. Zusätzlich wurden die Flächen des Oberhangs und des Unterhangs getrennt voneinander analysiert, da die Habitatqualität sich hier sehr stark unterscheidet. Der Wechsel des Beweidungssystems konnte nicht nur durch die Artenanzahl, sondern auch anhand der Zusammensetzung der Arten nachgewiesen werden. Nach vier Untersuchungsjahren war die Artenanzahl auf der Schweineweide am höchsten, gefolgt von der gemischten Rinder- und Schweineweide und am niedrigsten auf der Brache. Arten-turnover, welcher als zusätzlicher Indikator für Diversität diente, war am höchsten auf der Brache verglichen mit der Schweineweide und der Rinder- und Schweineweide. Die Entwicklung der Artenzusammensetzung konnte mit Hilfe einer Detrended Correspondence Analysis (DCA) dargestellt werden. Während sich die Artenzusammensetzung nach dem Wechsel des Beweidungssystems änderte, blieb der Einfluss der Hangneigung über die Jahre und Beweidungssysteme hinweg deutlich sichtbar.

Kapitel 4 behandelt den Einfluss traditioneller Managementmethoden (Brennen, Pflügen, sowie eine Kombination aus beiden) auf die Artenzusammensetzung von beweideten Flächen. Pflügen, und weniger häufig Brennen, sind geläufige Pflegemaßnahmen um die Verbuschung in beweideten mediterranen Dehesas zurück zu drängen. Sowohl die Flächen mit den unterschiedlichen Pflegemaßnahmen untereinander als auch diese Flächen im Vergleich zu den kontinuierlich beweideten Flächen ohne zusätzliches Management unterschieden sich nicht nur in der Artenanzahl, sondern auch in der Artenzusammensetzung. Die Artenzahlen aller Untersuchungsflächen lagen jedoch im letzten Jahr der Untersuchung wieder nahe beieinander. Da die Artenzusammensetzung bis zum Ende der Untersuchung für die unterschiedlich behandelten Flächen im Vergleich zu den beweideten Flächen ohne zusätzliche Pflegemaßnahme verschieden war, kann anhand einiger ausdauernden Arten von einer Art Gedächtnis der Vegetation bezüglich Störungen ausgegangen werden. Basierend auf der Frage, ob unterschiedliches Management der Weiden als auch die Hangneigung die Bodenfeuchtigkeit und damit auch die Artenzusammensetzung beeinflussen, wurde eine Analyse der Bodenfeuchtigkeit der unterschiedlich gemanagten Weiden sowie der Hangneigungen in die vorliegende Studie mit aufgenommen. Das Management hatte sowohl einen starken Einfluss auf die Wasserkapazität des Bodens als auch auf die Artenzusammensetzung und Artenanzahl. Zusätzlich wurde der Einfluss des Managements auf die Verbuschung hin untersucht. *Cistus* spec., als typische feuerangepasste Pflanzengattung des mediterranen Beckens, zeigte eine Zunahme auf den gebrannten sowie gebrannten und gepflügten Flächen im Vergleich zu den gepflügten und ausschließlich beweideten Flächen. Dies deutet die Probleme des Managements der Verbuschung mit den auf Weiden ungewollten Pflanzen nach einem Feuer an.

In häufig gestörten Habitaten, in welchen das Aussterben und die Neubesiedlung häufig sind, sind effektive Ausbreitungsmechanismen in Raum und Zeit essentiell für das Überleben von Pflanzenarten. Zusätzlich gewinnt die Ausbreitung durch Samen in Folge der Änderung der Landnutzung und damit einhergehend einer Zunahme der Landschaftsfragmentierung als auch der erwartete Klimawandel stärker an Bedeutung, da durch effektive Ausbreitungsmechanismen die (Wieder-) Besiedlung von Habitaten ermöglicht wird. Mediterrane Vegetation sollte insbesondere an der Ausbreitung von Samen durch Herbivore angepasst sein, da diese Ökosysteme eine lange Historie der Beweidung aufweisen. Aufgrund dessen wurde in Kapitel 5 die endozoochore Samenausbreitung durch zwei traditionell in der spanischen Dehesa gehaltenen Nutztierarten, nämlich Rindern und Schweinen, betrachtet. Dementsprechend wurden die in Rinder- und Schweinedung gekeimten Arten sowie die Anzahl deren Keimlinge untersucht. Eine große Bandbreite an Arten wurde durch den Dung beider Tierarten in teilweise hoher Anzahl an Keimlingen pro Art ausgebreitet. Obwohl die Anzahl der Keimlinge von Schweinedung etwa 30% geringer war als die vom Rinderdung, war der mit dem paired t-test getestete Unterschied nicht signifikant. Die Anzahl der Arten hingegen war in Schweinedung signifikant geringer verglichen mit Rinderdung. Demnach keimte zwar eine geringere Anzahl an Arten von Schweinekot, aber in teilweise wesentlich höherer Keimlingsanzahl pro Art. Damit müssen sowohl Schweine als auch Rinder als wichtige Ausbreitungsvektoren für die Vegetation einer mediterranen Dehesa betrachtet werden. Jedoch konnte kein Muster bzgl. der Samenmerkmale entdeckt werden, welches die Unterschiede in der Qualität und Quantität der endozoochoren Ausbreitung durch die beiden Tierarten beschreibt.

In mediterranem Grasland mit einer Dominanz einjähriger Arten spielt die Bodensamenbank eine entscheidende Rolle als Quelle des Keimlingsaufwuchs. Die Langlebigkeit von Samen in der Samenbank garantiert die Re-Kolonisierung von gestörten Habitaten nach der Beseitigung der Vegetation. Daher beschäftigt sich Kapitel 6 mit der Bodensamenbank von unterschiedlich gemanagten Weiden des Untersuchungsgebiets. Dabei wurden die Artenzahlen sowie die Anzahl der Keimlinge pro Art in zwei Bodenschichten, der oberen Bodenschicht von 0 - 5 cm und der tieferen Bodenschicht von 5 - 10 cm, verglichen. Insgesamt keimten 76 Arten aus den untersuchten Bodenproben. Die Anzahl der Arten variierte je nach Bodentiefe und dem Management der jeweiligen Weide. In der oberen Bodenschicht keimten bis zu 30 Arten aus den Bodenproben der gebrannten Weide bis hin zu 42 Arten aus den Bodenproben der Rinder- und Schweineweide. Aus den Bodenproben der tieferen Bodenschicht keimte mit bis zu 15 Arten aus den Bodenproben der gebrannten Weide bis hin zu 26 Arten aus den Bodenproben der Schweineweide insgesamt eine geringere Anzahl. Zum Vergleich der Ähnlichkeit der Artenzusammensetzung der Samenbank und der entsprechenden Vegetation wurde der Sørensen's similarity index herangezogen. Die Ähnlichkeit zwischen der Bodensamenbank und der Vegetation war mit 23 % bis zu 35 % für die obere Bodenschicht und 17 % bis zu 25 % für die tiefere Bodenschicht und den entsprechenden Vegetationsaufnahmen auf den unterschiedlich gemanagten Weiden insgesamt gering. Die Ähnlichkeit nahm mit zunehmender Störungsintensität ab. Dies kann als ein Leeren der Bodensamenbank nach Störungen durch eine damit verbundene erhöhte Keimungsrate interpretiert werden. Durch eine erhöhte Keimungsrate nach einer Störung würde der Anteil der dormanten, zum Zeitpunkt der Störung nicht keimfähigen Samen, verstärkt in der Samenbank übrig bleiben. Neben der Störung des Bodens und der Vegetation sollten sich auch die für das mediterrane Klima typischen fluktuierenden Niederschläge in der generell geringen Ähnlichkeit der Bodensamenbank und der aktuellen Vegetation niederschlagen. Starke Schwankungen der Niederschläge zwischen den Jahren und auch innerhalb eines

Jahres beeinflussen die Keimung sowie das Überleben der Keimlinge und können damit auch entscheidend die Zusammensetzung der Arten von einem Jahr auf das nächste beeinflussen. Während die aktuelle Vegetation stark von dem jährlichen Niederschlag abhängig ist, sollte die Bodensamenbank die Gesamtheit der Arten mit ausdauernder Samenbank über die Jahre hinweg repräsentieren. Die Ordination der Bodenproben und der Vegetationsaufnahmen macht ebenfalls die Unterschiede zwischen der aktuellen Vegetation und den Bodenproben deutlich. Demzufolge konnte zwar eine hohe Anzahl an Arten in den Bodenproben gefunden werden, jedoch konnte die erwartete Ähnlichkeit zwischen Vegetation und Samenbank aufgrund des hohen Störungsregimes und der Dominanz einjähriger Arten in der aktuellen Studie nicht gefunden werden.

Neben Beweidung stellt Feuer einen entscheidenden Faktor dar, welcher zur Gestaltung der mediterranen Ökosysteme beiträgt. Auch für die mediterrane Dehesa wird Feuer als ein Faktor gesehen, welcher einen entscheidenden Anteil an der Entwicklung des Ökosystems hatte und aufgrund der hohen Feuerfrequenz in Mediterranen Systemen auch heute noch hat. Für viele Arten ist Feuer als Filter für die Keimungsnische bekannt. Temperatur und Rauch gelten als verantwortlich für die Erhöhung der Keimungsrate bei einem breiten Spektrum an Arten. In Bezug darauf wurde in Kapitel 7 die Hypothese getestet, ob Feuer in der Entwicklung der Dehesa eine entscheidende Rolle spielte. Dafür wurde das Keimungsverhalten von 27 typischen Arten der Dehesa, welche sowohl Sträucher als auch Kräuter umfassen, mittels eines Laborexperiments auf ihre Hitze- und Rauchsensitivität untersucht. Anhand der Experimente konnten die 27 untersuchten Arten aufgrund ihres Keimungsverhaltens nach einer Hitzebehandlung und / oder Rauchbehandlung in vier Gruppen eingeteilt werden. Neun Arten zeigten eine erhöhte Keimungsrate nach der Hitzebehandlung (z. B. *Cistus ladanifer*, *Psoralea bituminosa*), und vier Arten nach der Rauchbehandlung (z.B. *Diplotaxis catholica*, *Sesamoides caniscens*). Während acht Arten indifferente Keimungsraten nach den Behandlungen zeigten (z.B. *Hedypnois cretica*, *Lavendula stoechas*), hatten sechs Arten zu geringe Keimungsraten für eine Eingruppierung (z.B. *Trifolium cherleri*, *Tuberaria guttata*). Insgesamt zeigten die in diesem Experiment getesteten Arten eine große zwischenartliche Varianz in ihren Reaktionen auf die Hitze- und Rauchbehandlungen. Die Ergebnisse lassen die Schlussfolgerung zu, dass der Einfluss des Managements Feuer als auch die zunehmende Anzahl an Wildfeuer einen erheblichen Einfluss auf die Artenzusammensetzung von Dehesa Grasland haben kann.

In Kapitel 8 werden abschließend die Ergebnisse im Gesamtkontext der Studie diskutiert. Basierend auf der Studie wird nachfolgender Untersuchungsbedarf identifiziert. Um Vorhersagen zur langfristigen Entwicklung des Untersuchungsgebietes aufgrund der Änderung in der Bewirtschaftung aufzudecken, sollte das Management als auch das Monitoring über einen längeren Zeitraum fortgeführt werden, um dadurch allgemeine Aussagen über die Vegetationsentwicklung treffen zu können. Um effektive Maßnahmen für den Erhalt dieses Lebensraumes zu schaffen, sollten zusätzlich Prozesse wie der zu erwartende Klimawandel als auch die zunehmende Fragmentierung der Landschaft mit in die Betrachtung einbezogen werden. Wenn Management die Widerstandskraft und Anpassungsfähigkeit von Mediterranen Arten zu einem sich ändernden Klima beeinflusst, spielt ein angepasstes Management eine entscheidende Rolle für das Überleben dieser Ökosysteme auf lange Sicht. Da effiziente Ausbreitungsmechanismen eine entscheidende Rolle sowohl in sich ändernden Ökosystemen als auch mit zunehmender Fragmentierung spielen mögen, sind weitere Studien notwendig, um generalisierbare funktionale Ergebnisse zu erhalten. Darauf basierend sollten Maßnahmen zum Erhalt dieser Lebensräume eingeführt werden, welche die bestehenden Ausbreitungsmechanismen fördern und erhalten.

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Appendices

Tab. A-1: Species presence / absence in pig and cattle dung (chapter 5), soil seed bank (chapter 6) and on cattle and pig pasture, pig pasture and fallow (chapter 3).

	cattle dung	pig dung	soil seed bank	cattle & pig pasture	pig pasture	fallow
Aira caryophyllea	x					
Anagallis arvensis	x		x	x	x	x
Anthyllis lotoides	x			x		x
Aphanes cornucopioides	x					
Arabidopsis thaliana	x					
Biserrula pelecinus	x		x	x	x	
Brachypodium distachyon		x		x	x	x
Briza minor	x					
Bromus diandrus	x					x
Bromus hordeaceus	x			x	x	x
Bromus tectorum	x					x
Capsella bursa-pastoris	x				x	
Cerastium glomeratum	x	x	x	x	x	x
Chaetonychia cymosa	x	x				
Chamaemelum fuscatum	x					
Chenopodium murale	x	x				
Cistus crispus	x		x			
Cistus salviifolius	x		x			
Coleostephus myconis		x	x	x		
Conyza albida	x	x				
Coronilla dura	x		x	x		x
Crepis foetida	x				x	x
Cynosurus cristatus	x					
Desmazeria rigida	x					
Diplotaxis catholica	x		x	x	x	x
Erodium botrys	x		x			
Erodium cicutarium	x					
Erodium moschatum	x			x	x	x
Erodium primulaceum	x	x	x	x		x
Euphorbia chamaesyce	x		x			
Euphorbia peplus		x				
Filago pyramidata	x			x	x	
Galium mollugo	x			x	x	x
Gastridium ventricosum	x		x	x	x	x
Gaudinia fragilis	x	x	x		x	x
Geranium molle	x		x	x	x	x
Hedypnois cretica	x			x	x	x
Heliotropium europaeum	x	x	x			
Hypochaeris glabra	x		x	x	x	
Illecebrum verticillatum	x		x		x	
Jasione montana	x		x			
Juncus bufonius	x	x	x			

Tab. A-1 continued.

	cattle dung	pig dung	soil seed bank	cattle & pig pasture	pig pasture	fallow
Leontodon longirrostris	x		x	x	x	
Lolium rigidum	x		x	x	x	x
Lythrum acutangulum	x					
Lythrum portula		x	x			
Malva sylvestris	x			x		
Medicago polymorpha	x	x		x	x	x
Melilotus elegans	x	x				
Misopates orontium	x		x	x	x	x
Ononis cintrana	x					
Ornithopus compressus	x		x	x	x	x
Papaver rhoeas	x					
Paronychia echinulata	x	x		x		
Plantago coronopus	x	x	x	x	x	
Plantago lagopus	x		x	x	x	x
Poa annua	x	x	x			
Polycarpon tetraphyllum	x	x				
Polypogon maritimus	x	x				
Psoralea bituminosa	x					
Pulicaria paludosa	x					
Ranunculus tripartitus	x					
Raphanus raphanistrum	x		x		x	x
Rumex bucephalophorus	x		x	x	x	x
Senecio vulgaris		x	x			
Sesamoides canescens	x					
Sherardia arvensis	x			x	x	x
Silene gallica	x		x	x	x	x
Sisymbrium officinale	x		x	x	x	x
Sonchus asper	x	x			x	
Sonchus oleraceus	x	x		x	x	x
Sonchus tenerrimus		x	x	x	x	
Spergularia rubra	x	x	x	x	x	
Stellaria pallida	x					
Tolpis barbata	x		x	x	x	x
Torilis nodosa	x		x		x	
Trifolium arvense	x		x	x		
Trifolium campestre	x	x	x	x		
Trifolium cherleri	x	x	x	x	x	x
Vulpia ciliata	x			x	x	
Vulpia geniculata	x	x		x	x	x

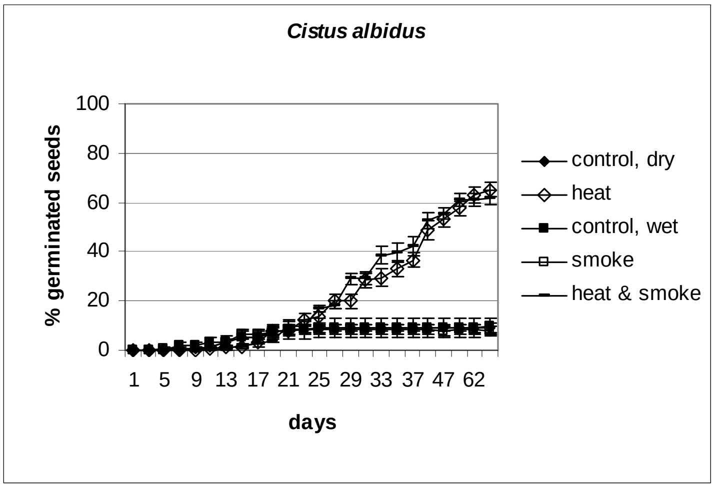
Tab. A-2: Species presence in vegetation (veg), soil seed bank (ssb) and both in vegetation and soil seed bank (veg / ssb). Included are data from cattle and pig pasture burned, cattle and pig pasture upper slope, cattle and pig pasture lower slope, pig pasture without shrub cover and pig pasture with shrub cover (see also chapter 6).

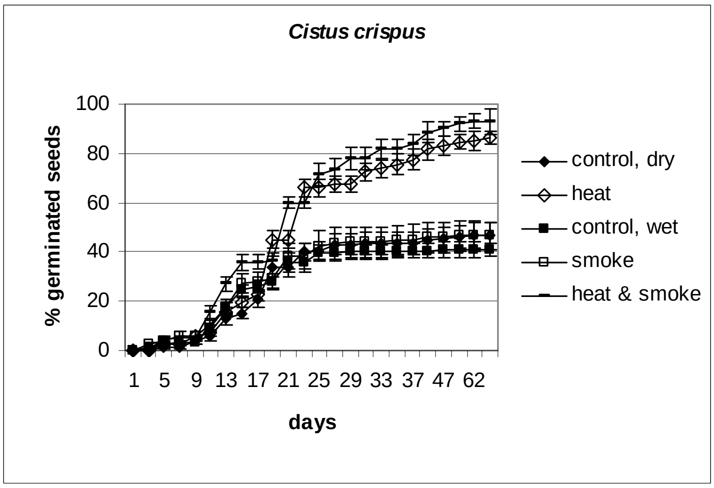
species	presence
Aegilops geniculata	veg
Agrostis castellana	ssb / veg
Alyssum simplex	veg
Anagallis arvensis	ssb / veg
Andryala integrifolia	veg
Anthemis arvensis	ssb / veg
Anthyllis lotoides	veg
Aphanes cornucoioides	ssb / veg
Aphanes microcarpa	veg
Astragalus cymbicarpos	ssb / veg
Avena barbata subsp. lusitanica	veg
Barbarea intermedia	ssb
Bellardia trixago	veg
Bellis annua	veg
Biserrula pelecinus	ssb / veg
Brachypodium distachyon	veg
Brassica barrelieri	ssb / veg
Briza maxima	veg
Bromus diandrus	veg
Bromus hordeaceus	veg
Bromus matritensis	veg
Calendula arvensis	veg
Cardamine hirsuta	veg
Carex acuta	ssb
Carthamus lanatus	veg
Centaurea melitensis	veg
Centaurium maritimum	ssb
Cerastium glomeratum	ssb / veg
Chrysanthemum coronarium	veg
Chrysanthemum segetum	ssb / veg
Cistus crispus	ssb / veg
Cistus ladanifer	ssb
Cistus salvifolius	ssb / veg
Cleome violacea	veg
Coleostephus myconis	ssb / veg
Coronilla dura	ssb / veg
Corrigiola litoralis	ssb / veg
Crepis foetida	veg
Cuscuta planiflora	ssb / veg
Diplotaxis catholica	ssb / veg
Echium plantagineum	ssb / veg
Erodium botrys	ssb / veg
Erodium moschatum	veg
Erodium primulaceum	ssb / veg
Eryngium campestre	veg
Euphorbia chamaesyce	ssb
Euphorbia exigua	veg
Evax lusitanica	ssb / veg
Filago lutescens	ssb / veg
Fumaria calcarata/petteri	veg
Galactites tomentosa	veg
Galium mollugo	veg
Gastridium ventricosum	ssb / veg
Gaudinia fragilis	ssb / veg

species	presence
Genista hirsuta	veg
Geranium molle	ssb / veg
Gymnostyles stolonifera	ssb
Gynandriris sisyrinchium	veg
Hedypnois cretica	veg
Helianthemum aegyptiacum	veg
Heliotropium europaeum	ssb
Herniaria scabrida	ssb
Hordeum leporinum	veg
Hypericum perforatum	ssb
Hypochaeris glabra	ssb / veg
Illecebrum verticillata	ssb / veg
Jasione montana	ssb / veg
Juncus bufonius	ssb / veg
Juncus capitatus	veg
Lamarckia aurea	ssb / veg
Lathyrus angulatus	veg
Leontodon longirrostris	ssb / veg
Leontodon salzmannii	veg
Linaria amethystea	veg
Linum bienne	veg
Lolium rigidum	ssb / veg
Lotus conimbricensis	ssb / veg
Lupinus micranthus	veg
Lythrum portula	ssb
Malva sylvestris	veg
Matricaria recutita	veg
Medicago minima	veg
Medicago polymorpha	veg
Misopates orontium	ssb / veg
Muscari comosum	veg
Ononis cintrana	veg
Ononis repens	veg
Ornithogalum umbellatum	veg
Ornithopus compressus	ssb / veg
Ornithopus pinnatus	ssb / veg
Orobanche minor	veg
Parentucellia latifolia	veg
Paronychia argentea	ssb / veg
Paronychia echinulata	veg
Petrorhagia velutina	veg
Plantago afra	veg
Plantago bellardii	ssb / veg
Plantago coronopus	ssb / veg
Plantago lagopus	ssb / veg
Plantago lanceolata	ssb
Poa annua	ssb
Poa bulbosa	veg
Pulicaria odora	veg
Ranunculus arvensis	veg
Ranunculus paludosus	veg
Raphanus raphanistrum	ssb / veg
Rostraria cristata	veg
Rumex angiocarpus	ssb / veg

Tab. A-2 continued.

species	presence
Rumex bucephalophorus	ssb / veg
Salvia verbenaca	ssb
Scorpiurus vermiculatus	ssb / veg
Sesamoides canescens	veg
Sherardia arvensis	veg
Silene gallica	ssb / veg
Sisymbrium officinale	ssb / veg
Sonchus oleraceus	veg
Sonchus tenerrimus	ssb / veg
Spergularia rubra	ssb / veg
Stachys arvensis	veg
Stipa capensis	veg
Teesdalia coronopifolia	veg
Thapsia villosa	veg
Tolpis barbata	ssb / veg
Trifolium angustifolium	veg
Trifolium arvense	ssb / veg
Trifolium campestre	ssb / veg
Trifolium cherleri	ssb / veg
Trifolium scabrum	ssb / veg
Trifolium stellatum	veg
Trifolium striatum	veg
Trifolium strictum	veg
Trifolium subterraneum	veg
Trifolium sylvaticum	veg
Trifolium tomentosum	veg
Tuberaria guttata	ssb / veg
Vicia lutea subsp. lutea	veg
Vicia sativa subsp. cordata	veg
Vulpia ciliata	veg
Vulpia geniculata	veg





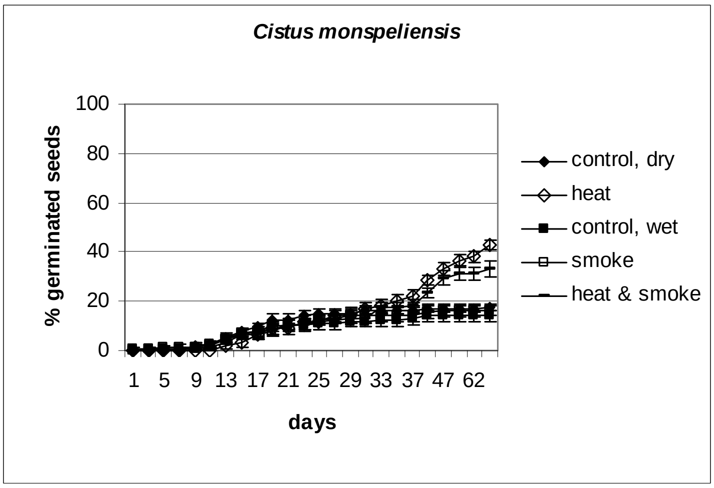


Fig. A-1: Group A: Cumulative number of germinated seeds for ten species with enhanced germination after heat and heat & smoke treatment. For description of treatments see Tab. 7.2.

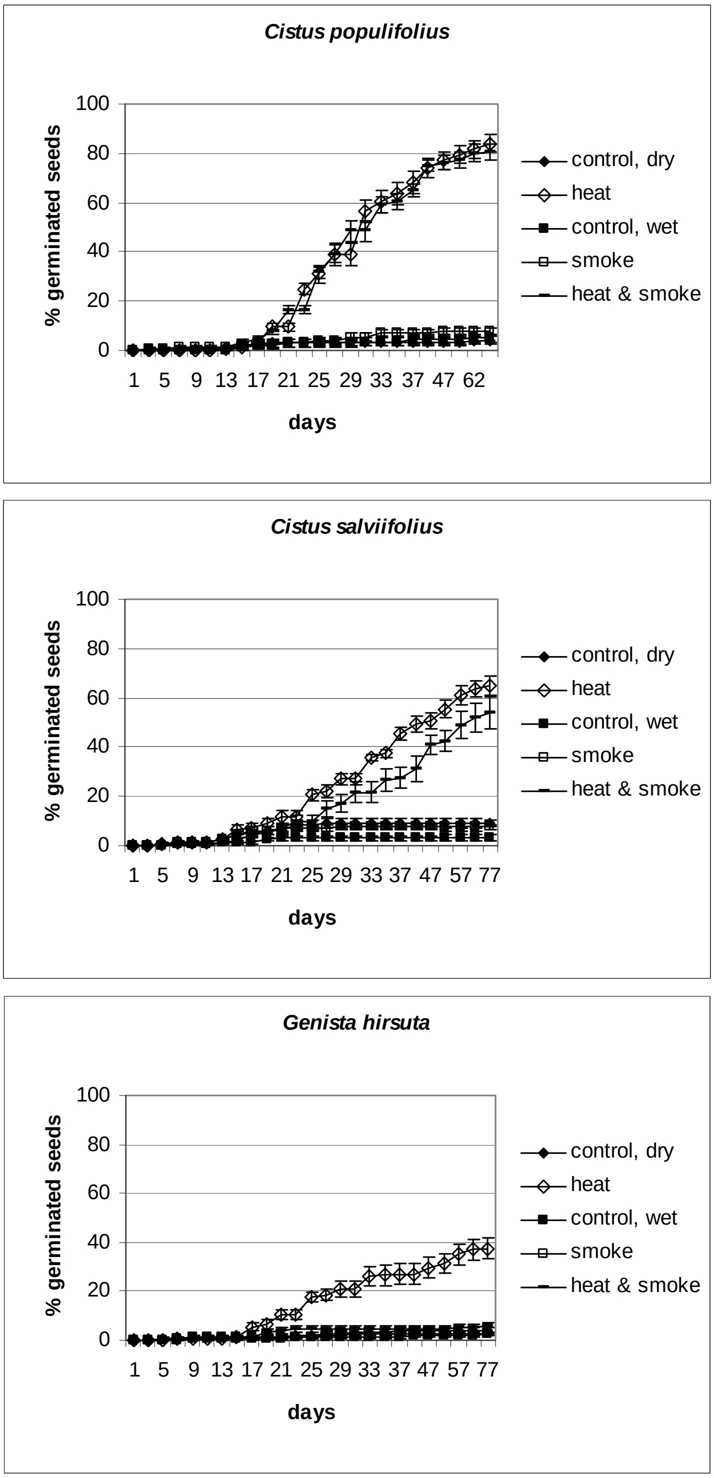


Fig. A-2: Group A: Cumulative number of germinated seeds for ten species with enhanced germination after heat and heat & smoke treatment. For description of treatments see Tab. 7.2.

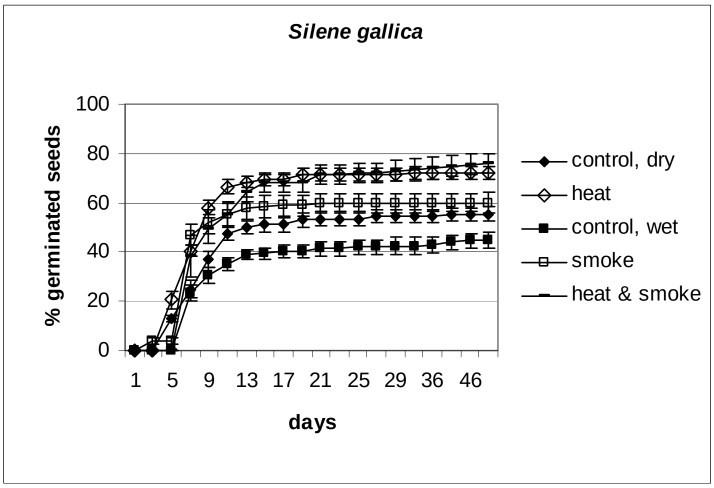


Fig. A-3: Group A: Cumulative number of germinated seeds for ten species with enhanced germination after heat and heat & smoke treatment. For description of treatments see Tab. 7.2.

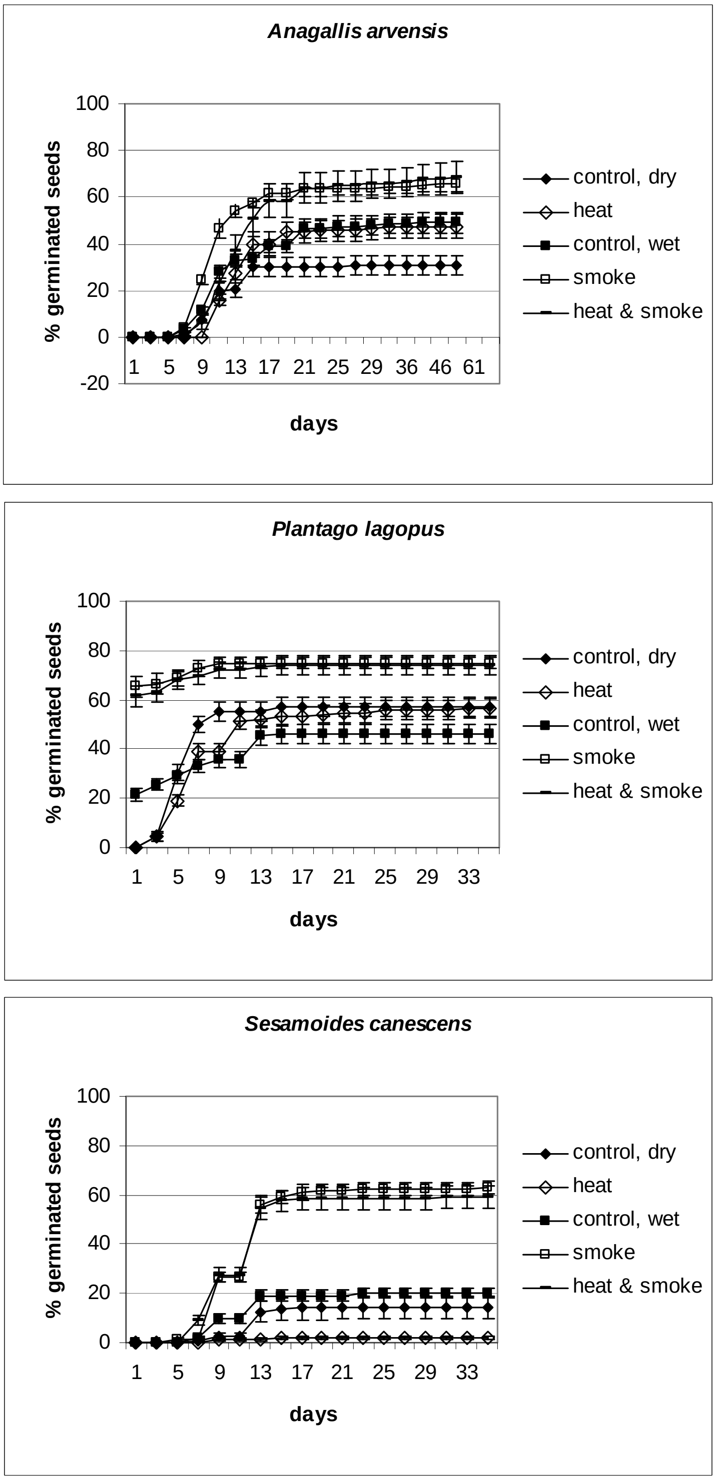
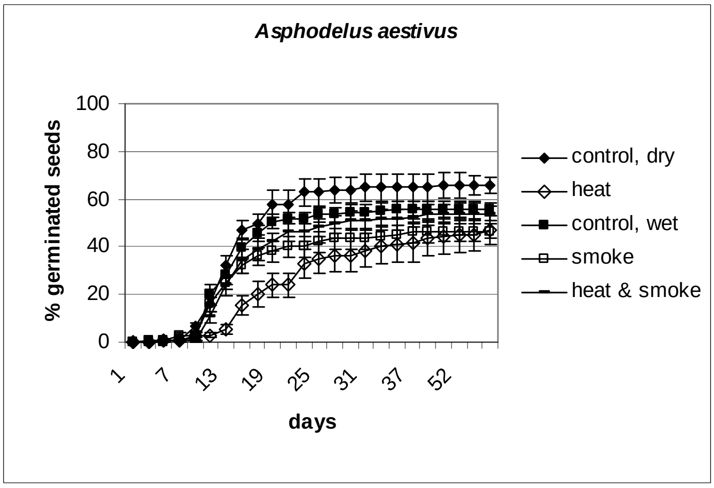
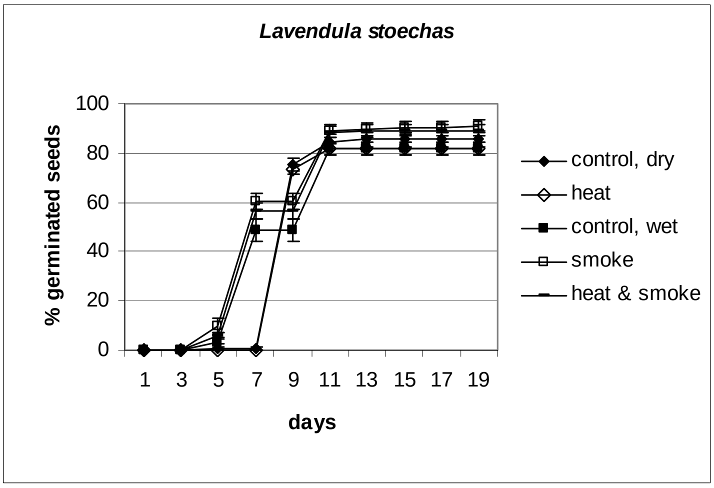


Fig. A-4: Group B: Cumulative number of germinated seeds for four species with enhanced germination after smoke and smoke & heat application. For description of treatments see Tab. 7.2.





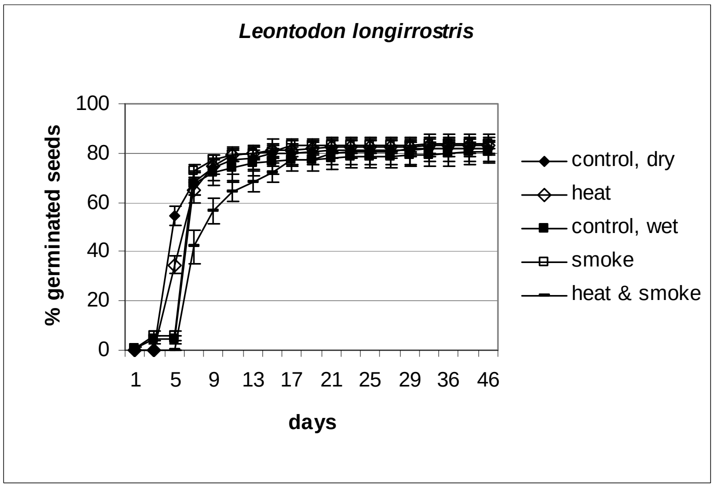
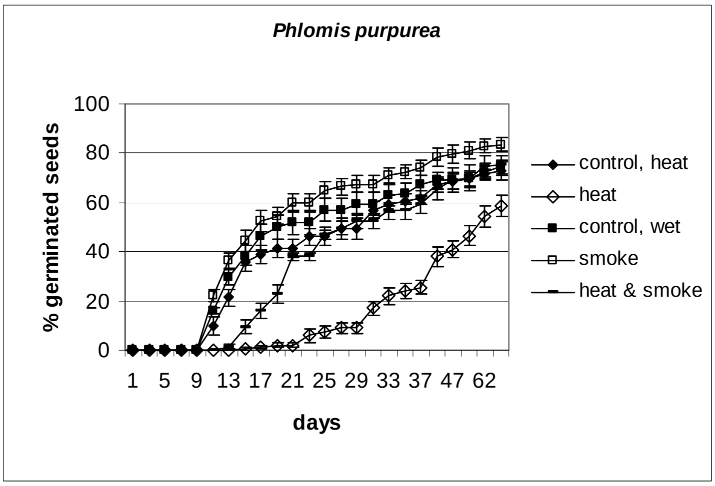
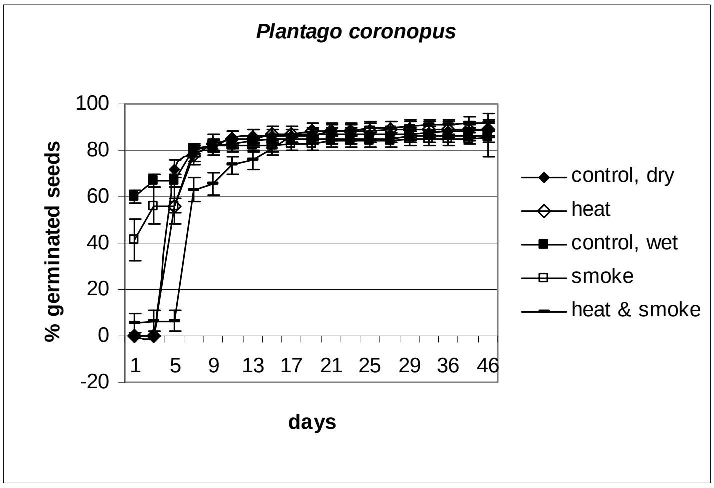


Fig. A-5: Group C: Cumulative number of germinated seeds for eight species without any difference in germination between control and applications. For description of treatments see Tab. 7.2.





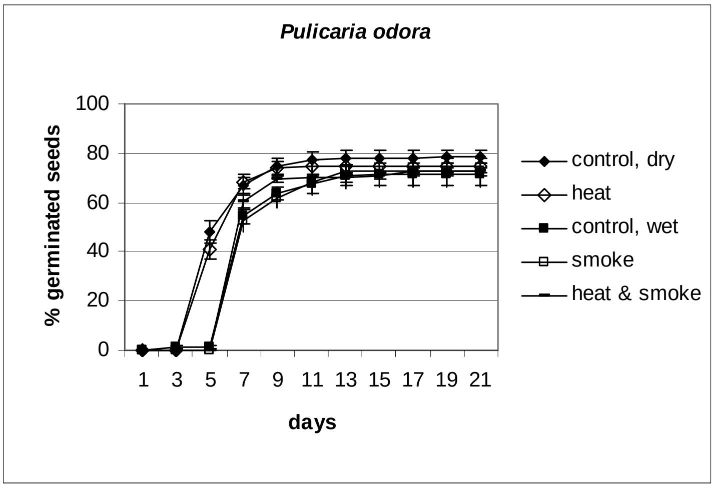


Fig. A-6: Group C: Cumulative number of germinated seeds for eight species without any difference in germination between control and applications. For description of treatments see Tab. 7.2.

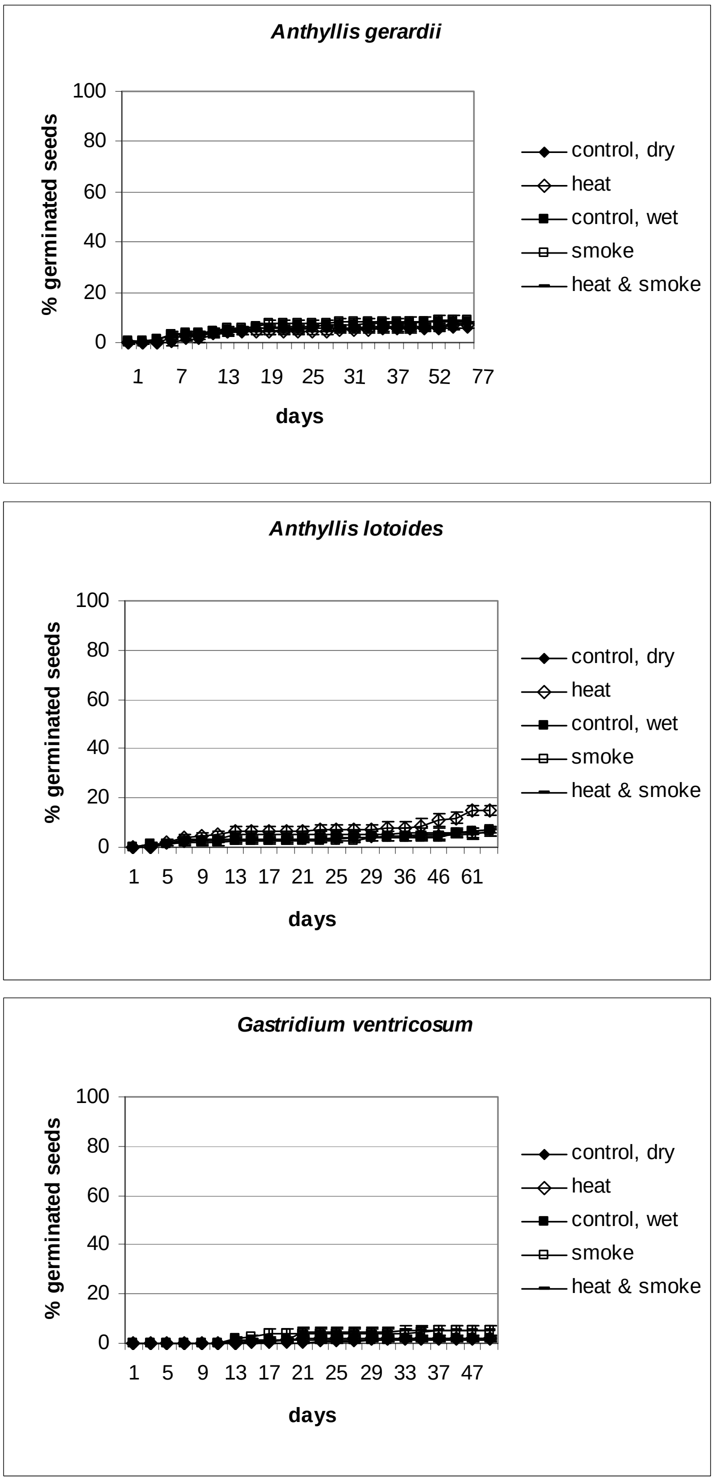
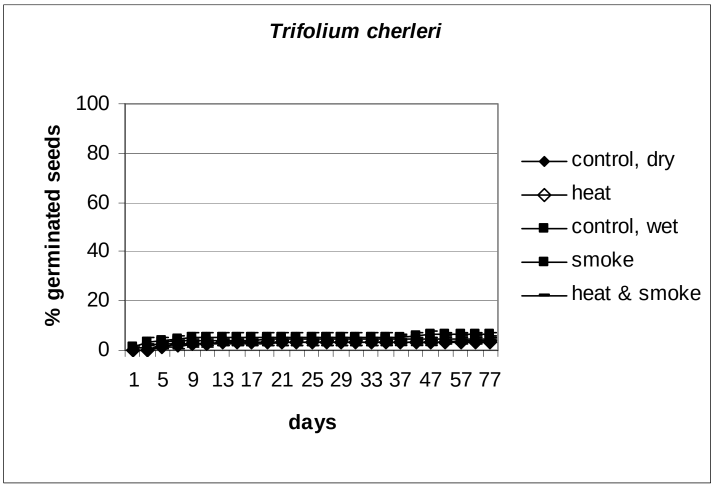
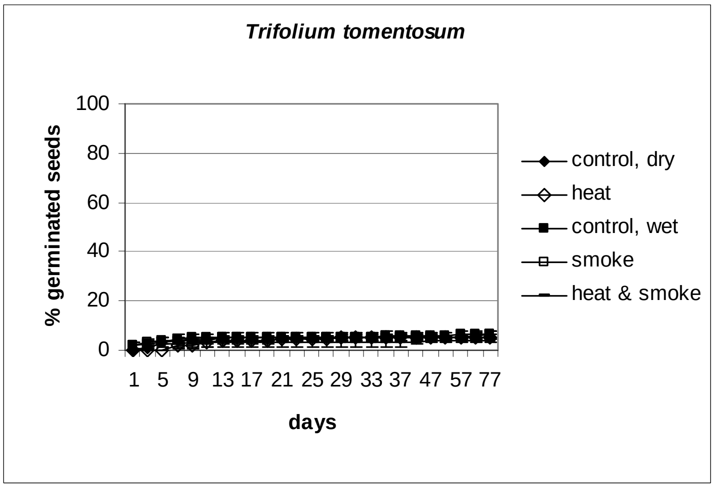


Fig. A-7: Group D: Cumulative number of germinated seeds for five species with too low germination rates to interpret any adaptation. For description of treatments see Tab. 7.2.





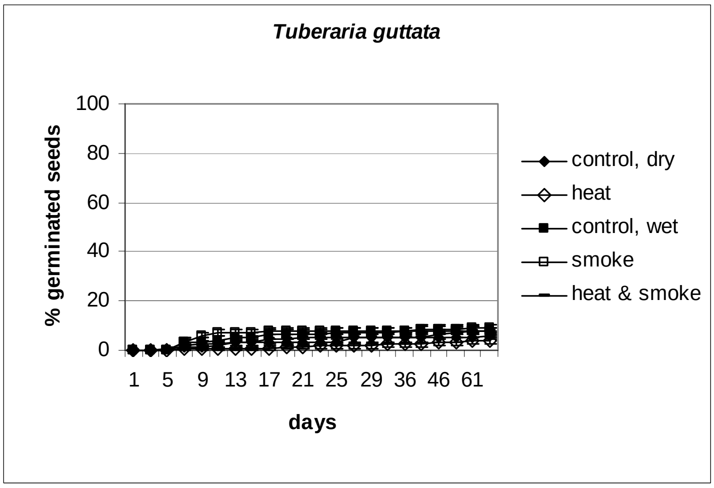


Fig. A-8: Group D: Cumulative number of germinated seeds for five species with too low germination rates to interpret any adaptation. For description of treatments see Tab. 7.2.

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