

# Seed contents of sika deer (*Cervus nippon*) dung and the fate of seeds in a temperate short grassland in an urban park in Japan

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## Abstract

Many studies have suggested the positive effects of grazing by large herbivorous mammals on seed dispersal, but little is known about how herbivores could affect the fate of ingested seeds. This study examined the effects of seed ingestion by sika deer (*Cervus nippon*) on seed fate in a temperate grassland established in an urban park long resided by high densities of sika deer. I compared species composition and seasonal traits of seed abundance and maturity in the grassland community with those in deer fecal pellets. In total, 27 herbaceous species were observed, including the predominant *Zoysia japonica*. Seed phenology and production differed among the three dominant species (*Z. japonica*, *Digitaria violascens*, and *Hydrocotyle maritima*). Pellets contained at least 26 species of herbaceous seeds, and their abundance differed among species. Of the 26 species, 15 were observed in the vegetation at the study site. The peak of seed abundance in pellets for the dominant species appeared 1 month after the peak of inflorescence production (but most of the inflorescences were immature and susceptible to digestion) and consequently corresponded to the peak of mature inflorescence. Because sika deer are likely to ingest seeds at any maturity stage in the grassland and immature seeds are less hardened, ingested immature seeds can suffer great losses. The results suggested that the survival of germable seeds with great losses of immature seeds may be a factor determining which plant species can be successfully dispersed by herbivores.

**Key words:** fecal pellets, maturity of inflorescences, seed ingestion, seed phenology, sika deer grazing, vegetation

## INTRODUCTION

Many plant species are dispersed by herbivorous animals (e.g., Welch 1985, Malo and Suárez 1995, Pakeman et al. 2002). Several studies have indicated that large herbivores act as potentially important seed dispersal agents (Gill and Beardall 2001, Myers et al. 2004, Cosyns and Hoffmann 2005, von Oheimb et al. 2005). After ingestion by large herbivores, seeds undergo chemical and physical attacks such as chewing, rumination, and digestion. Small, hard-coated seeds with no obvious specialized diaspores are less likely to be damaged during passage

through the digestive tract of ruminants and are more likely to be dispersed in dung, whereas larger seeds are heavily damaged (Janzen 1984, Gill and Beardall 2001, Bruun and Fritzboeger 2002, Heinken et al. 2002, Pakeman et al. 2002, Myers et al. 2004, Mouissie et al. 2005). The number of germable seeds in dung varies seasonally, and this seems to reflect seed production at the grazing site (Malo and Suárez 1995). However, previous studies on seed dispersal have focused primarily on the results of germination experiments with seeds excreted by her-

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bivores (e.g., Malo and Suárez 1995, Pakeman et al. 2002, Cosyns and Hoffmann 2005). Such approaches may underestimate both species and seed numbers (Couvreur et al. 2004). The dung of herbivores may also contain many seeds that cannot germinate as a result of differences in germination conditions among plant species (Grime et al. 1988, Ishikawa 2011) and/or in seed conditions such as immaturity, death, or dormancy. Grazing of immature seeds (including flower buds and flowers) or death of seeds by passing through the digestive tract may preclude the next generation. Thus, seed dispersal by herbivores can involve negative effects on plant populations and communities.

The sika deer (*Cervus nippon* Temminck) is a dominant large wild herbivore in Japan and consumes a range of plant materials, including bamboo leaves, grasses, tree leaves, and twigs and nuts (Miura 2005). In recent years, the population of sika deer has increased in many parts of Japan, often destroying endemic vegetation (e.g., Okuda and Nakane 1990, Shimoda et al. 1994, Akashi and Nakashizuka 1999, Maesako et al. 2007). Yamashiro and Yamashiro (2006) showed that seeds are dispersed by sika deer on a subtropical island; the deer carried many small graminoid seeds from open habitats to both open and forest habitats, and, thus, the deer probably contributed to grassland expansion. Recent elevated densities of sika deer may have a greater effect on plant communities than ever before through seed ingestion and dispersal as well as through grazing and browsing. In Japan, a *Zoysia*-dominated community develops in the most heavily grazed places (Takatsuki 2009).

Plant species growing in short grasslands produce reproductive organs on short stems close to the leaves, and the reproductive organs are very small and intermingled with foliage. The sika deer is a grazer (Hofmann 1985), and the reproductive organs are thus likely to be ingested by the deer together with the leaves and stems at any maturity stage in the short grasslands. If sika deer continually and nonselectively graze various herbaceous plants at different developmental stages in the community, two hypotheses arise on the fate of seeds grazed by the deer: (i) sika deer dung may contain many small seeds of various herbaceous species growing at the grazing site, and (ii) immature seeds grazed by sika deer together with germable seeds may disappear during passage through the digestive tract.

The objectives of this study were to test these hypotheses by (i) comparing species composition and abundance of each species at the grazing site with those in sika deer dung and (ii) comparing the seasonal traits of production

and maturity of reproductive organs (inflorescences) of dominant plant species in the community at the grazing site with those of the abundance and maturity of seeds in sika deer dung on a temperate grassland established in an urban park, Nara Park. At the same study site, Ishikawa (2010) suggested that although mature seeds of the dominant *Z. japonica* and *H. maritima* were excreted by sika deer with no reduction or enhancement of germination rate, numerous immature seeds, including flower buds and flowers, may also be ingested and are likely to suffer significant damage as a result of digestive processes. If so, seasonal traits in production and maturity of seeds in the grassland would not correspond to those of the abundance and maturity of seeds in dung.

## MATERIALS AND METHODS

### Study site

Nara Park (approximately 660 ha) is a large urban park, which is located in the city of Nara (34°40' N, 135°50' E) in western Japan. The area has a warm-temperate climate with a mean annual rainfall of 1,338 mm. Mean annual temperature is 14.6°C, with an average monthly minimum of 3.8°C in January and a maximum of 26.6°C in August (1971-2000) (Japan Meteorological Agency 2011). The climax vegetation in this area is a lucidophyllous forest of *Castanopsis cuspidata* (Thunb.), Schottly and oak species such as *Quercus glauca* Thunb., *Quercus myrsinifolia* Blume, and *Quercus sessilifolia* Blume.

In Nara Park, sika deer have a home range of approximately 12 ha for females and approximately 8 ha for males and show daily activity throughout this range (Miura 1977). The deer move between open land and forest and graze in the grasslands and rest in the forests (Fukunaga and Kawamichi 1975, Fukunaga 1976). The deer have long been protected for religious reasons, and they have no natural predators. During the 1940s, the deer population in the park declined to no more than 80 individuals as a result of poaching to provide food during the war, but by 1965 it had recovered to approximately 900, and has ranged from 1,000 to 1,300 for the last 30 years (Foundation for the Protection of Deer in Nara Park 2011). The current population level appears to be at or close to the park's carrying capacity (Torii and Tatsuzawa 2009). As a result of heavy deer impacts for many years, Nara Park has a unique ecosystem and a distinctive landscape; large open areas are covered with *Zoysia*-type grasslands (Takatsuki 1980), and some species that are unpalatable

or harmful to sika deer, such as *Nageia nagi* (Thunb.) Kuntze and *Pieris japonica* (Thunb.) D. Don ex G. Don subsp. *japonica*, grow thickly in some places. Additionally, tree seedlings, twigs, and leaves within reach of the sika deer are browsed in the patchy forests that remain in the park, forming a so-called browse line (Crawley 1983).

This study was conducted in the Tobihino area (approximately 1.9 ha), which is a flat part of southeastern Nara Park (Ishikawa 2010, 2011). The deer density is particularly high (between 430 and 5,500 individuals/km<sup>2</sup>) (Foundation for the Protection of Deer in Nara Park unpublished data) in the Tobihino area. The Tobihino area is covered with grasslands dominated by *Z. japonica* (Takatsuki 1980) and is one of the grazing sites in Nara Park. In the Tobihino area, sika deer depend principally on graminoids (mainly *Z. japonica*) during the growing season, but the importance of *Z. japonica* for the deer decreases greatly with the onset of the dormant season, when other forbs take its place (Takatsuki and Asahi 1977, 1978). All plant species in the grasslands have been dwarfed as a result of trampling and grazing by the high density of sika deer. Furthermore, wild boars (*Sus scrofa leucomystax*) have been observed digging up the soil (Maesako 2002), which may be an important disturbance factor in the grassland community. In late July 2000, the boars stripped off layers of the grassland in some places at the study site.

### Census and analysis of vegetation

Censuses for plant species composition and percent cover of each species present were performed from May 2000 to December 2003. Vegetation height was assessed from May to November 2001, February to November 2002, and January to December 2003. Five permanent circular plots (each 10 m<sup>2</sup>) were established along a straight line for periodic vegetation censuses. There was a separation of 10 m between the center of one plot and the center of the next plot. In each plot, two quadrats (each 50 cm × 50 cm) were established randomly during each census. Thus, at each census, 10 quadrats were assessed for vegetation height, plant species composition, and the percentage cover of each species present in the plot.

Vegetation height, as an index of the vegetation successional stage, at each census was represented by the mean height from the 10 quadrats. Significant changes in vegetation height during the study period and in the mean vegetation height at each census were tested among months and years by means of a two-way analysis of variance (ANOVA) in the Generalized Linear Models

module of SPSS ver. 11.5J for Windows (SPSS Inc., Chicago, IL, USA).

For each species, percent cover was visually evaluated using 11 ranks (from 0% to 100% at 10% intervals). Those species whose mean cover in the 10 quadrats exceeded 20% were defined as dominant species; those with 1-10% cover were defined as species with low cover, and those with < 1% cover were defined as rare species. In the present study, the vegetation structure was represented by a combination of vegetation height and percent cover.

### Seed phenology and the production of inflorescences on dominant species

The abundance and maturity of the inflorescences of the following three dominant species were evaluated in both the vegetation and sika deer fecal pellets. *Zoysia japonica* is a perennial creeping grass with short leaves that produces emergent flowering stems and grows in sunny, disturbed places (Kasahara 1968, Numata and Yoshizaga 1971). *Hydrocotyle maritima* is a perennial creeping forb with small leaves and short stems and grows in places with high soil moisture content. It produces flowering stems shorter than its leaf stalks. *Digitaria violascens* is an annual tufted grass that grows in sunny places and produces flowering stems with 5-10 ears per inflorescence.

Censuses were performed from May 1999 to January 2004; *Z. japonica* was surveyed for 5 years starting in 1999, *H. maritima* in 2002 and 2003, and *D. violascens* in 2003. In the five fixed circular plots, the number of inflorescences was counted and their degree of maturity was visually determined for the three species. The size and number of quadrats per plot were determined to include as many inflorescences as possible for each species: two for *Z. japonica* (each 50 cm × 50 cm) and one each for *H. maritima* (each 50 cm × 50 cm) and *D. violascens* (each 50 cm × 25 cm). To avoid a risk of double-counting, each inflorescence was distinguished by sticking toothpicks on the soil surface close to each inflorescence after it was counted. Seed phenology was defined using four maturity stages for the inflorescences and seeds: pre-flowering (in *Z. japonica* and *D. violascens*, the heads broke through the leaf sheaths and began to grow, and in *H. maritima*, flower buds were formed); flowering; immature seeds (seeds and inflorescences were still green); and mature seeds (seeds and inflorescences turned brown). It was assumed that the number of inflorescences counted at each census represented the number produced during the interval between each census and the next minus the

number consumed by sika deer.

### Sampling of sika deer pellets and seeds contained in the pellets

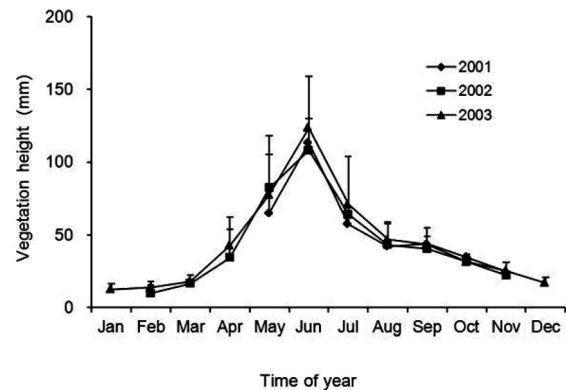
To estimate mean fecal pellet mass, two pellets were collected from each of five pellet groups on each of six sampling occasions between May and August ( $N = 60$ ). A pellet group was defined as a group of pellets produced by a single defecation. The pellets were dried in a convection oven (85°C, 48-h), weighed, and the volume of each pellet was estimated by approximating a cylinder. The mean number of pellets per pellet group was calculated from a total of 16 pellet groups in May and August 2000.

Sika deer fecal pellets were collected approximately every 2 weeks from April to July and monthly from August to November from May 1999 through November 2001. Only fresh pellets were collected, after removal of any surface material that might have contaminated them with uningested seeds. Because excretion of seeds by sika deer reaches a peak about 2 days after ingestion (Takatsuki 2006), the time lag between occurrence of seeds in these fresh pellets and seed phenology can be considered negligible. To determine the species composition and density of seeds per pellet, two (in 1999) or four pellets (in 2000 and 2001) were collected from each of five pellet groups on each sampling occasion (a total of 90 pellets in 1999 and 220 pellets each in 2000 and 2001). The pellets were air-dried and maintained at room temperature (20-25°C). Each pellet was soaked in water in a Petri dish until it had absorbed enough water to soften (approximately 1-h), and was then carefully picked apart with tweezers. Seeds were separated from the pellets under a stereomicroscope (40-100× magnification) and then identified to the species level (where possible), according to specimens in a seed herbarium and specimens collected *in situ*. Seeds were then classified into three categories: woody plant, graminoid, or forb.

## RESULTS

### Species composition, vegetation height, and plant community dynamics

At least 30 plant species were recorded during the study period: 27 species were herbaceous plants belonging to 13 families (10 graminoids, 15 forbs, one grass, and one herb), one species was a bamboo, and two species were woody seedlings (Table 1). Of the 27 species, the



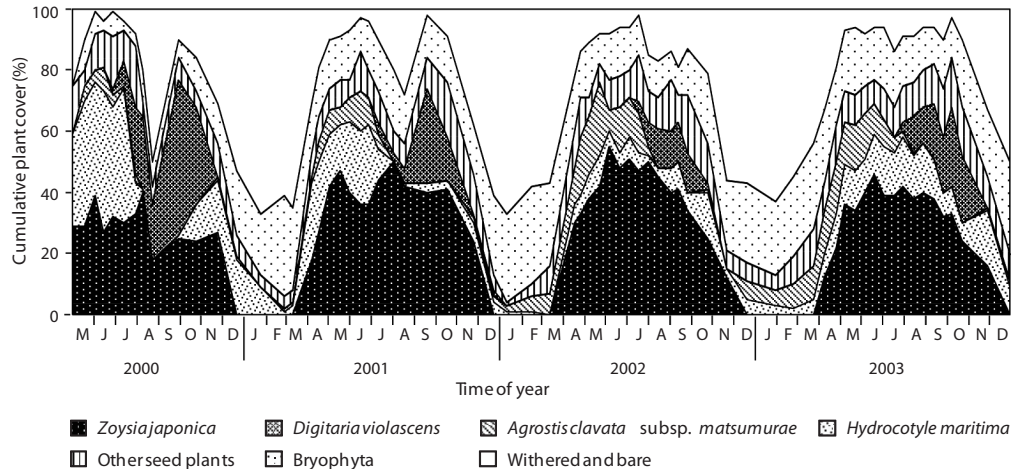
**Fig. 1.** Seasonal changes in the average vegetation height. Values are means  $\pm$  standard deviation ( $N = 10$  on each date, except 20 September 2001, for which  $N = 8$ ).

dominant species were *Z. japonica* (Poaceae), *H. maritima* (Umbelliferae), *D. violascens* (Poaceae), and *Agrostis clavata* Trin. subsp. *matsumurae* (Hack. ex Honda) Tateoka (Poaceae). Six other herbaceous species had low cover, and the remaining 17 species were rare. The site also contained withered plants and patches of bare ground.

Vegetation height began to increase in March, reached a peak of 100-120 mm in June (the heights of the flowering stems of *Z. japonica* and *A. clavata* subsp. *matsumurae*), and then declined to a minimum of 10-15 mm in winter (Fig. 1). A significant difference was observed in vegetation height among months (two-way ANOVA;  $F = 67.28$ ,  $df = 11$ ,  $P < 0.001$ ) but not among years ( $F = 2.06$ ,  $df = 2$ ,  $P > 0.05$ ), and there was no year  $\times$  month interaction ( $F = 0.59$ ,  $df = 5$ ,  $P > 0.05$ ). The 3-year trend of low vegetation height during the winter indicates that no woody plants became established at the study site.

The total plant cover also showed a periodic trend (Fig. 2). The cover exceeded 70% from spring to autumn, except for a drop to approximately 50% in August 2000 and declined sharply in winter to less than 20% (excluding bryophytes). The cover of the four dominant species accounted for 60-80% of the plant community during the growing season. Among the dominant species, *Z. japonica* showed the most distinct periodic trend. The cover of *Z. japonica* was consistently high (> 20%) from spring to autumn throughout the study period. *Digitaria violascens* and *A. clavata* subsp. *matsumurae* had a typical annual cycle each year. *Digitaria violascens* cover peaked in autumn and exceeded 20% in 2000, 2001, and 2003. *Agrostis clavata* subsp. *matsumurae* cover increased from near-zero levels in autumn and reached a peak from spring to early summer. It exceeded 20% only in 2002, when the cover of *H. maritima* declined. *Hydrocotyle maritima*





**Fig. 2.** Seasonal changes in the mean and cumulative plant species cover of plant species. Plant species other than the four dominant species are combined into "other seed plants" and areas with withered or no plants are included in "withered and bare."

showed a less obvious periodic trend among the 4 years, but the trends were similar in 2000 and 2001 and again in 2002 and 2003. *Hydrocotyle maritima* cover exceeded 20% around the first peak (from spring to summer) in 2000 and 2001 but declined to < 20% after August 2001.

### Seed phenology and production of *Z. japonica*, *D. violascens*, and *H. maritima* inflorescences

The maximum number of *Z. japonica* inflorescences per square meter ranged from 81.2 (in May 2000) to 249.6 (in May 2002), that of *D. violascens* was 3,541.3 in October 2003, and that of *H. maritima* was 498.4 in June 2002 and 1,370.4 in June 2003.

Because of the similarity among phenologies, only *Z. japonica* and *H. maritima* data for 2003 are presented in a figure (Fig. 3). *Zoysia japonica* inflorescences appeared in April and increased rapidly until the beginning of May then decreased gradually (Fig. 3a). The peak abundance of total and mature-seed inflorescences occurred in early May and late June, respectively. The proportion of pre-flowering inflorescences was highest in April and decreased rapidly, followed by flowering starting in late April, immature-seed inflorescences starting in early May, and mature-seed inflorescences starting in late May (Fig. 3b). The proportion of mature-seed inflorescences increased gradually from late May, and approximately 90% of inflorescences were mature in late June.

*Digitaria violascens* inflorescences appeared at the beginning of October and increased rapidly until late October, then decreased gradually (Fig. 3c). The peak abundance of mature-seed inflorescences occurred in

early November. The proportion of pre-flowering inflorescences was highest in October, followed by flowering inflorescences from shortly after the appearance of pre-flowering inflorescences and immature- and mature-seed inflorescences from late October onward (Fig. 3d). The proportion of mature-seed inflorescences increased gradually from late October, and approximately 70% of inflorescences were mature in mid November.

*Hydrocotyle maritima* inflorescences appeared in May and increased gradually until the end of June, then decreased gradually until autumn, with a peak in the number of mature-seed inflorescences in mid-July (Fig. 3e). The mature-seed inflorescences accounted for < 20% of the total from June to August. In contrast to *Z. japonica* and *D. violascens*, all inflorescence maturity stages were consistently present on each sampling date from June to September, and the relative proportion of each maturity stage was relatively constant throughout the study period (Fig. 3f). Thus, *H. maritima* formed flower buds and dropped seeds soon after maturity.

### Seeds in sika deer fecal pellets

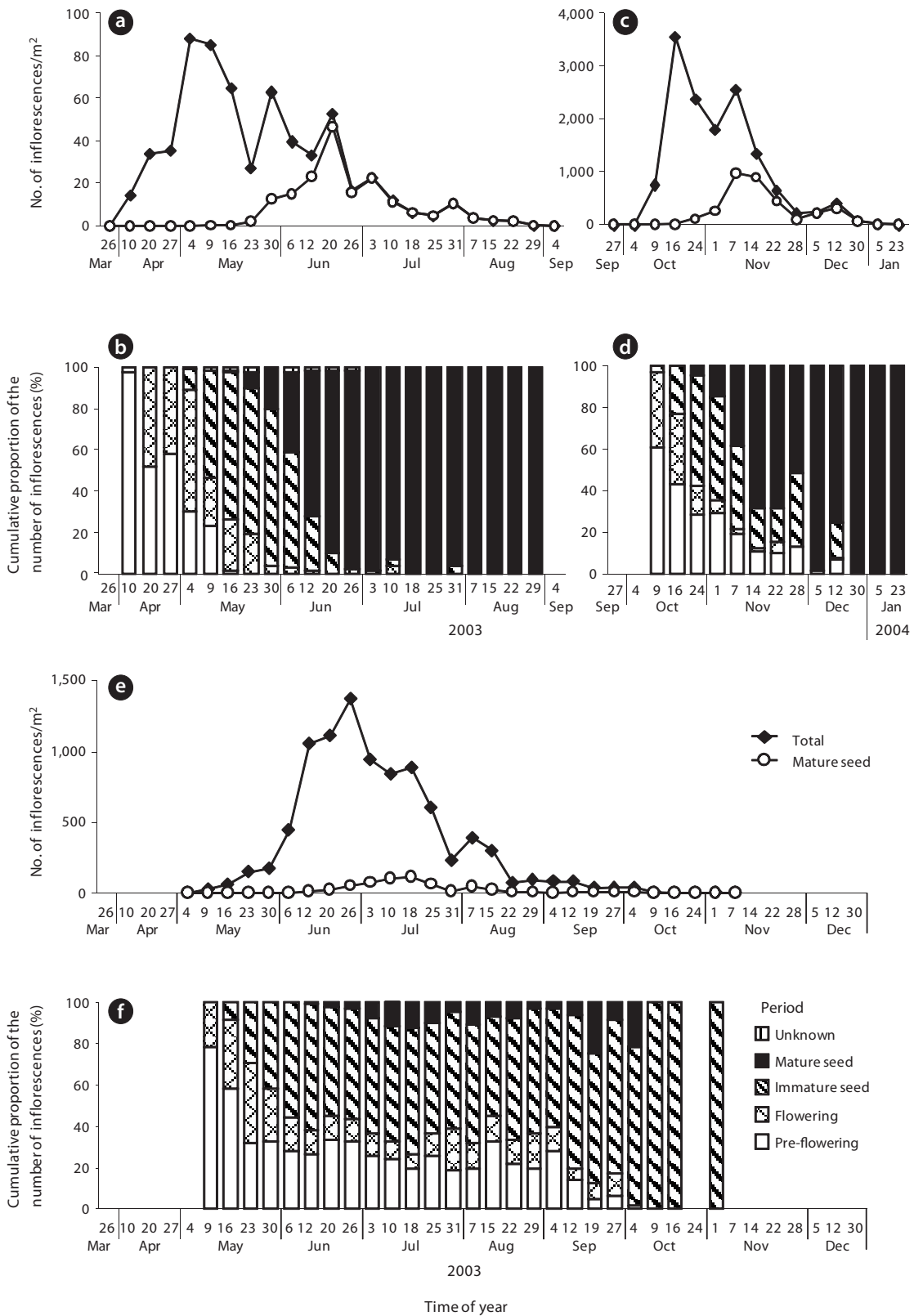
The mean number of pellets per defecation was  $60.4 \pm 14.1$  (mean  $\pm$  standard deviation,  $N = 16$ ; range, 33 to 99). The mean volume per pellet was  $0.62 \pm 0.17$  cm<sup>3</sup>, and the dry mass per pellet was  $0.19 \pm 0.05$  g ( $N = 60$ ).

In total, 530 pellets (approximately 100 g dry weight) from 155 fecal pellet groups were collected during the study. Overall, 2,257 seeds belonging to at least 26 species (11 graminoids and 15 forbs) from 15 families were extracted from the pellets (Table 1). Of the 26 species,

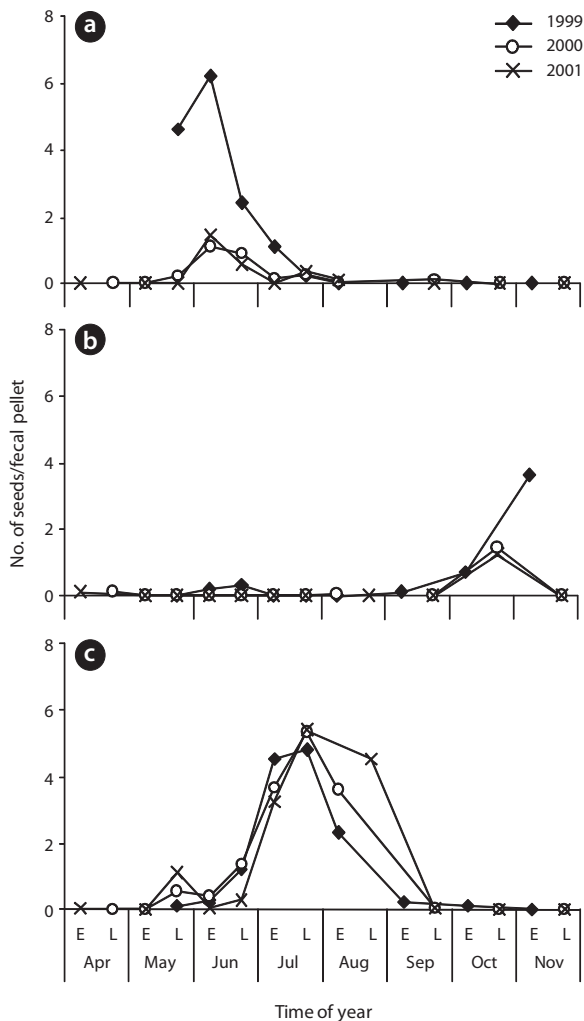
**Table 1.** Herbaceous plant species growing in the plant community at the study site from May 2000 to December 2003, and the maximum number of seeds per sika deer fecal pellet and the total number of seeds contained in the pellets (530 pellets from May to November 1999 and from April to November in 2000 and 2001) collected in the Tobihino area of Nara Park

Family name	Species name	Life form	Maximum	Total
<b>&lt;Species growing in the plant community at the study site&gt;</b>				
<b>Dominant species</b>				
Poaceae	<i>Digitaria violascens</i> Link	Graminoid	5	108
Poaceae	<i>Zoysia japonica</i> Steud.*	Graminoid	10	249
Poaceae	<i>Agrostis clavata</i> Trin. subsp. <i>matsumurae</i> (Hack. ex Honda) Tateoka	Graminoid	5	54
Umbelliferae	<i>Hydrocotyle maritima</i> Honda*	Forb	16	645
Bryophyta	Unknown	-	-	-
<b>Species with low cover</b>				
Poaceae	<i>Poa annua</i> L.	Graminoid	5	111
Poaceae	<i>Paspalum thunbergii</i> Kunth ex Steud.	Graminoid	-	-
Poaceae	<i>Pleioblastus</i> sp.	-	-	-
Cyperaceae	<i>Fimbristylis dichotoma</i> (L.) Vahl var. <i>tentsuki</i> T. Koyama*	Graminoid	6	41
Cyperaceae	<i>Cyperus brevifolius</i> (Rottb.) Hassk. var. <i>leiolepis</i> (Franch. et Sav.) T. Koyama*	Graminoid	11	126
Caryophyllaceae	<i>Sagina japonica</i> (Sw.) Ohwi	Forb	22	597
Asteraceae	<i>Gnaphalium japonicum</i> Thunb.	Forb	1	3
<b>Rare species</b>				
Iridaceae	<i>Sisyrinchium rosulatum</i> E.P. Bicknell	Forb	1	1
Juncaceae	<i>Juncus tenuis</i> Willd.*	Graminoid	8	131
Poaceae	<i>Miscanthus sinensis</i> Andersson	Graminoid	-	-
Poaceae	Unknown	Graminoid	-	-
Polygonaceae	<i>Persicaria longiseta</i> (Bruijn) Kitag.	Forb	6	21
Caryophyllaceae	<i>Arenaria serpyllifolia</i> L.	Forb	-	-
Caryophyllaceae	<i>Stellaria media</i> (L.) Vill.	Forb	3	59
Caryophyllaceae	<i>Stellaria uliginosa</i> Murray var. <i>undulata</i> (Thunb.) Fenzl	Forb	-	-
Caryophyllaceae	<i>Cerastium glomeratum</i> Thuill.	Forb	-	-
Rosaceae	Unknown	Forb	-	-
Clusiaceae	<i>Hypericum laxum</i> (Blume) Koidz.	Forb	1	7
Fabaceae	<i>Kummerowia striata</i> (Thunb.) Schindl.	Forb	-	-
Scrophulariaceae	<i>Mazus miquelii</i> Makino	Forb	-	-
Plantaginaceae	<i>Plantago asiatica</i> L.*	Forb	2	16
Asteraceae	<i>Conyza</i> sp.	Forb	-	-
Monocotyledon	Unknown	-	-	-
Dicotyledon	Unknown	-	-	-
Seedlings of woody plants	Species 1	-	-	-
	Species 2	-	-	-
<b>&lt;Species that were not observed at the study site&gt;</b>				
Juncaceae	<i>Luzula capitata</i> (Miq.) Miq. ex Kom.	Graminoid	1	4
Poaceae	<i>Isachne nipponensis</i> Ohwi	Graminoid	1	6
Poaceae	<i>Cynodon dactylon</i> (L.) Pers.	Graminoid	1	2
Poaceae	<i>Alopecurus aequalis</i> Sobol. var. <i>amurensis</i> (Kom.) Ohwi	Graminoid	1	2
Polygonaceae	<i>Persicaria lapathifolia</i> (L.) Delarbre	Forb	3	9
Polygonaceae	<i>Persicaria</i> sp.	Forb	2	5
Brassicaceae	<i>Capsella bursa-pastoris</i> (L.) Medik.	Forb	1	1
Fabaceae	<i>Trifolium repens</i> L.	Forb	1	3
Violaceae	<i>Viola verecunda</i> A. Gray*	Forb	1	3
Boraginaceae	<i>Trigonotis peduncularis</i> (Trevir.) Benth. ex Hemsl.	Forb	1	1
Solanaceae	<i>Physalis alkekengi</i> L. var. <i>franchetii</i> (Mast.) Makino	Forb	1	2
Unknown				50

\*Species found in sika deer dung collected in the Tobihino area in June and August of 2000 and 2001 (Ishikawa 2011).



**Fig. 3.** Seasonal changes in the number of inflorescences and the proportion of inflorescences at each maturity stage for (a, b) *Zoysia japonica*, (c, d) *Digitaria violascens*, and (e, f) *Hydrocotyle maritima*.



**Fig. 4.** Number of seeds of (a) *Zoysia japonica*, (b) *Digitaria violascens*, and (c) *Hydrocotyle maritima* per sika deer fecal pellet. E, early; L, late.

58% (15 species) corresponded to species previously observed at this site. The total number of seeds from these 15 species accounted for 96.1% of all the seeds in pellets. The maximum number of seeds per pellet was 29 in May 2001. Of the identified species, no intact woody-plant seeds were present. The seeds of *Z. japonica* were the largest of all species collected from the pellets during the study. Many crushed *Castanopsis* nutshells occurred in the pellets in autumn.

The abundance of seeds extracted from the pellets differed among herbaceous species, but could be roughly classified into three groups according to the period of seed occurrence: spring-summer, midsummer, and autumn. When analyzing the species with a monthly mean of more than three seeds per pellet during the study period, *Z. japonica* and *Sagina japonica* (Sw.) Ohwi were found in pellets during the early summer, *H. maritima* in

midsummer, and *Cyperus brevifolius* (Rottb.) Hassk. var. *leiolepis* (Franch. et Sav.) T. Koyama and *D. violascens* in autumn. The seed abundances of *Z. japonica*, *D. violascens*, and *H. maritima* in pellets varied seasonally (Fig. 4). The pellets contained *Z. japonica* seeds from May to July (Fig. 4a), *D. violascens* seeds from October to early November (Fig. 4b), and *H. maritima* seeds from May to August (Fig. 4c). The peak abundance of seeds in pellets occurred in June for *Z. japonica*, in late October and early November for *D. violascens*, and in July and August for *H. maritima*. In May, all seeds of *H. maritima* collected from pellets were immature and small (approximately 0.8 mm).

## DISCUSSION

### Vegetation structure and dynamics of the herbaceous plant community

The vegetation of the Japanese archipelago, which mostly experiences a warm-humid temperate climate, is dominated by forests, and most of the existing grasslands have been established under conditions of ongoing physical disturbance or stress, such as mowing or grazing (Tagawa 1973). Under heavy intense grazing by large mammals, the vegetation of such grasslands develops as a community dominated by *Z. japonica* (Takatsuki 2009). For example, on Kinkazan Island in northeastern Japan, regeneration of the beech forests has been strongly suppressed by heavy sika deer browsing (Takatsuki and Ito 2009), and *Z. japonica* has rapidly invaded areas where deer density was high (Takatsuki and Gorai 1994, Takatsuki and Ito 2009). At the study site, where the sika deer population seems close to the site's carrying capacity (Torii and Tatsuzawa 2009), continual heavy grazing and trampling by the deer may be responsible for maintaining short herbaceous communities as the biotic climax stage and a dynamic equilibrium of the dominant species, such as *Z. japonica*, *H. maritima*, and *D. violascens*.

Obvious declines in vegetation cover of all species occurred in August 2000 due to partial stripping off of the herbaceous vegetation layers by wild boars in late July and an unusually low amount of rain in August (only 18 mm). As a result of the low precipitation, the vegetation's ability to produce new biomass decreased. Although part of the area that was disturbed seriously by the boars was invaded by bryophyte species, most of the vegetation at the study site recovered after this combination of biotic and abiotic disturbances.



## Seed contents of sika deer pellets

Seeds of at least 26 herbaceous species were extracted from sika deer pellets. In the same study area, seedlings of nine of the 26 species (five graminoids and four forbs) and an additional four forb species (*Duchesnea chrysantha* [Zoll. et Moritzi] Miq. [Rosaceae], *Oxalis corniculata* L. [Oxalidaceae], *Clinopodium gracile* [Benth.] Kuntze [Lamiaceae], and *Mazus pumilus* [Burm. f.] Steenis [Scrophulariaceae]) emerged from sika deer dung in June and August 2000 and 2001 (Ishikawa 2011). Thus, viable seeds of 13 herbaceous species, including *Z. japonica* (Kitagawa 1988, Takatsuki 2006), were excreted by sika deer at the study site. Because sika deer graze on a wide variety of plants (Miura 2005) and deer densities are high in many parts of Nara Park, it is likely that many plant species other than those collected from fecal pellets in this study are excreted by the deer.

The species composition of seeds contained in fecal pellets generally reflected the vegetation at the study site; at least 58% of all species (15 of 26 species) at the study site were contained in sika deer fecal pellets, and the total number of seeds of the 15 species accounted for 96.1% of all seeds in the pellets. On a subtropical island in southern Japan, graminoid seeds dominate sika deer pellets, and more than 90% of them belonged to Cyperaceae, which are dominant in one of the foraging areas on this island (Yamashiro and Yamashiro 2006). These results reflect correlations between the abundance of the species in large herbivore dung and that in the foraging area (Couvreur et al. 2005). Although the number of seeds collected was very small (38 of 2,257 seeds), 42% of all species (11 of 26) in pellets could not be observed growing at the study site. Thus, sika deer also graze in other parts or outside of Nara Park and imported seeds from those areas to the study site.

The seed contents of pellets tended to be abundant for the dominant plant species in the community; many seeds of the dominant species *Z. japonica*, *D. violascens*, and *H. maritima*, were contained in pellets. However, the seed abundance in pellets did not necessarily reflect plant abundance in the community. For example, the total number of seeds of *H. maritima* and *S. japonica* contained in pellets was larger than that of the predominant *Z. japonica*. This may be attributed to differences in seed production per unit area and/or in the length of the seed production period between plant species. In this study, *H. maritima* had a larger production of inflorescences per unit area and a longer period of seed production than those of *Z. japonica*. Having more seeds may increase

the probability of ingestion and increase the effectiveness of excretion via the digestive tract of sika deer at this site. Although *S. japonica* was not a dominant species, the maximum number of seeds per pellet was largest of all plant species. Seeds of *S. japonica* are considerably smaller (0.4 mm) (Nakayama et al. 2000) than those of *Z. japonica* (2.7 mm) (Ishikawa 2010). In previous studies, the majority of seeds excreted by sika deer (30 of 35 species) are < 2 mm long (Yamashiro and Yamashiro 2006) and the germable seeds dispersed by white-tailed deer (81% of the germinations) are < 1 mm long (Myers et al. 2004). Having smaller seeds may increase the probability of survival during passage through the digestive tract.

## Comparison between seed phenology and seeds in pellets

In Nara Park, *Z. japonica* heads from April to May and the seeds mature from May to June (Kitagawa 1988), and this phenology agrees with that of the present study. Other species also showed particular seasonal patterns of seed production; *D. violascens* headed from early October to early December and the seeds matured from late October, whereas *H. maritima* produced flower buds from May to September and the seeds matured from June to October. The peak abundance of mature inflorescences occurred in late June for *Z. japonica*, in early November for *D. violascens*, and in July for *H. maritima*. The ripening and germination rates of mature *Z. japonica* seeds rose from early June, and those of *H. maritima* were high from late July to late August (Ishikawa 2010). In contrast to *Z. japonica* and *D. violascens*, *H. maritima* had all stages of inflorescence maturity, and the relative proportion of mature-seed inflorescences accounted for < 20% from June to August.

Based on the results of seed production and seed abundance in pellets for *Z. japonica*, *D. violascens*, and *H. maritima* at the study site, the peak seed abundance in pellets for a given species corresponded to the peak abundance of mature inflorescences for that species but did not correspond to the peak abundance of the total of all maturity stages of inflorescences, as most seeds were still immature at that time. Immature inflorescences (flower buds, flowers, and immature seeds) are so soft that they may be digested when passing through the digestive tract. When most *Z. japonica* inflorescences were immature in the grassland from late May to early June, more than 80% of seeds excreted by sika deer had no albumen (Ishikawa 2010). Therefore, when the seed coat develops to some extent, immature or empty seeds may

be tolerant of ingestion and be excreted during earlier periods of seed maturity. However, even if the immature seeds were excreted, they cannot germinate because they have not yet completed their development (Ishikawa 2010). Although mature-seed inflorescences of *H. maritima* were < 20% of the total inflorescence abundance in the community in July and August, more than 90% of the seeds excreted by the deer had mature albumen (Ishikawa 2010). Therefore, whereas ripened seeds may have tolerance to ingestion by sika deer, immature or empty seeds were probably crushed and digested.

Previous studies on seed dispersal by large herbivores (Malo and Suárez 1995, Pakeman et al. 2002, Cosyns and Hoffmann 2005, Couvreur et al. 2005) have not considered the loss of immature reproductive organs caused by grazing. The comparison between seed phenology in the community and seeds in sika deer pellets data in this study suggests that numerous reproductive organs may be consumed at immature stages by grazing deer, and that germable seeds excreted by the deer may be a slight part of seed production in the plant community. When fertile *Z. japonica* seeds were fed to sika deer, 38% were retrieved from dung (Takatsuki 2006). Thus, considering the destruction of young reproductive organs, the ratio of excreted seeds to ingested reproductive organs would be greatly less than 38%. The present study suggests that seed dispersal by large herbivores may be accompanied by heavy consumption of young reproductive organs and that not only small seed size but also the survival of germable seeds with great losses of young reproductive organs during passage through the digestive tract may be factors determining which species can successfully be dispersed by herbivores. The ingestion of seeds by sika deer is likely to affect the relative abundance of species in the plant community and will have a primary effect on the maintenance of component plant populations in Nara Park, as well as grazing and trampling.

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