



Analysis of effects of burning in grasslands with quantifying succession stages by life-history traits in Kirigamine, central Japan

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Abstract

To quantitatively analyze the effects of burning, we conducted a vegetation survey in the grasslands in Kirigamine, central Japan. We classified each species into stages of succession based on the life-history traits of the species and defined the score of the species in each stand based on the classification. We weighted the scores with a ν -value, the product of coverage and height in the quadrat, and summed them to calculate the index of dynamic status. With these indices, we were able to quantitatively compare the stands in the study area and discern minute differences between the stands with different lengths of restoration periods since the disturbance of burning. These indices correlated with the ν -value of trees, suggesting that the disturbance of burning seemed to affect the trees in the stand. We then calculated the growth of the tree species *Pinus densiflora* to evaluate its contribution to the index of dynamic status.

Key words: Effects of prescribed burning, Grassland succession, Life-history trait, Quantitative analysis

INTRODUCTION

Disturbance to plant communities alters the species composition of the stands (Connell 1978, Petraitis et al. 1989). Stands without artificial disturbance would flourish in succession. However, it is difficult to conduct a vegetation survey in a stand without artificial disturbance. Assuming that ideal succession would proceed under circumstances without artificial disturbance, Numata (1961, 1969) proposed a degree of succession (DS) to quantitatively evaluate how plant succession would proceed. He studied the quantitative evaluation of the dynamic process of plant stands based on the life-history traits of constituent species, because he believed that differences among the life-history traits of constituent species would drive stand succession.

Numata (1962) applied his idea to propose an index of grassland conditions to diagnose the degree of grazing in grasslands. Subsequently, Nakamura et al. (2000) applied

this idea and proposed a stand quality index to quantify the degree of disturbance caused by over-grazing in the grasslands of Inner Mongolia. However, when Numata (1961) gave scores to species based on the classification of their life-history traits, the number of his categories was only four: annual herb, perennial herb, shrub, and tree. Therefore, using the DS, we were not able to quantitatively separate minute differences between grassland stands with and without disturbances such as prescribed burning in the same stages. Moreover, it was difficult to discern small differences in the length of the restoration period since the prescribed burning.

Here, we propose a more detailed system for classifying the life-history traits of species that grow in Kirigamine semi-natural grasslands. Consequently, we were able to separate minute differences among the stands, thereby quantifying the status of grasslands. Our category system

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is based on field experiments of secondary succession conducted by Hayashi (1977, 1992, 2003).

Hayashi concluded that an ideal succession consists of eight stages. When succession proceeds, the dominant species may subsequently be altered. Therefore, the number of alternations of the dominant species until climax is eight. He uses the word "stage" as follows. Following the initial denuding of the plot, the first dominant species gradually appears (the first stage). As succession proceeds, the first dominant species is gradually replaced by a second dominant species (the second stage). The third, fourth, fifth, sixth, seventh, and eighth species become dominant subsequently (the third, fourth, fifth, sixth, seventh and eighth stage, respectively). He predicted the years $Y(i)$ from the initial denuding of the plot until the i^{th} stage in an ideal succession as follows: $Y(1)=1$, $Y(2)=2$, $Y(3)=4$, $Y(4)=8$, $Y(5)=16$, $Y(6)=32$, $Y(7)=64$, and $Y(8)=128$.

We assigned a score to each species as follows. First, we ascertained the life-history traits of the relevant species. Second, we assigned these species to the appropriate stage after considering the coincidence of life-history traits. Third, we assigned a score to each species. This score is the value equivalent to $Y(i)$.

To assign scores, we must determine the stages of succession to which the species belong. In this report, we determined the life-history traits of species by field observation and references. Consequently, we were able to reduce years of work related to determining the life-history traits of each species through our experiments. Therefore, we have been able to classify species in the stand into the eight stages of succession to assign scores.

STUDY SITE AND METHODS

Study site

The study site was on a gradual slope that was at least 1000 ha in width (Kurihara et al. 2002). The landscape was grasslands with *Miscanthus sinensis* as the dominant species. Until the 1960s, people living in that area collected grass for making compost and cattle food (Kurihara et al. 2002). The study site is situated south of Mt. Kurumayama (36°6'11"N, 138°11'49"E, 1925 m a.s.l.).

The mean annual temperature is 6.5°C and the mean annual precipitation is 1281 mm. Kira's warmth index is 52°C-month and the cold index is -41°C-month (KiNOA 2012). The soil is black humic soil originating from volcanic ash (Suzuki, personal communication).

Treatments of study plots and methods

The study plots consisted of five plots: A, B, C, D, and E. Study plots A, B, and C are situated within 1 km of each other. Study plot D is situated about 4 km east of Study plot C and Study plot E is about 4 km south of Study plot B. Study plots A, B, C, and D are situated at ca. 1600 m a.s.l. The local government of Suwa City and the landowners managed the times and places of the prescribed burning and tree cutting in Study plots A, B, and C. They conducted prescribed burning in spring 2005, 2006, 2007, and 2012 in Study plot A, which is ca. 7 ha wide. In 2012, we conducted vegetation surveys of the quadrats of Study plot A at the end of June (Subplot A1), July (Subplot A2), August (Subplot A3), and September (Subplot A4). Study plot B is ca. 12 ha wide. We divided Study plot B into Subplots B1 (ca. 6 ha) and B2 (ca. 6 ha), because the government and landowners conducted prescribed burning in Subplot B1 in spring 2008 and tree cutting in Subplot B2 in autumn 2008. Study plot C was ca. 6 ha wide and they conducted prescribed burning there in spring 2009. Study plot D consisted of Subplots D1 (ca. 2 ha), D2 (ca. 2 ha), D3 (ca. 1 ha), and D4 (ca. 2 ha). The landowners of D1 conducted prescribed burning in Subplot D1 in the spring of every year. Ski companies governed Subplots D2 and D3, so they conducted mowing without removing the mowed grass in Subplot D2 in the autumn of every year and tree cutting without removing the cut trees in Subplot D3 in the autumn of every year. We left Subplot D4 without treatment from 1967 to autumn 2012. In Study plot E, situated at ca. 1300 m a.s.l., *Pinus densiflora* forests surrounded the grassland with *M. sinensis* as a dominant species. Study plot E, which is as wide as ca. 1 ha, is situated within the grassland. The local government of Nagano Prefecture built enclosures to protect endangered insects in Study plot E so that they managed to survive the plant *Hemerocallis vespertina*. Enclosure 1 was ca. 0.3 ha and Enclosure 2 was ca. 0.06 ha. The government mowed and removed the mowed grass in June 2011 and June 2012 in Enclosure 1, where we set Subplot E1. We left Enclosure 2 without treatment, where we set Subplot E2. We set Subplot E3 outside the enclosures and left it untreated.

In each subplot, we arbitrarily placed 1 m × 1 m quadrats so that the distance between the quadrats was greater than 5 m (Okutomi and Itow 1967). The numbers of quadrats we placed in each subplot were 10 in Subplot A, 12 in Subplot B1, 12 in Subplot B2, 11 in Subplot C, 17 in Subplot D1, 6 in Subplot D2, 4 in Subplot D3, 9 in Subplot D4, 6 in Subplot E1, 6 in Subplot E2, and 6 in Subplot E3. We measured the maximum height (cm) and visually es-

estimated the coverage (%) of the quadrats of every species growing in the quadrat and the total coverage (%) of the quadrats. We conducted vegetation surveys of Study plots B, C, D, and E between the end of August and the end of September 2012. On 25 Sep 2012, we clipped the above-ground biomass of the constituent species in a 1 m × 1 m quadrat near Study plot A and dried them for 48 h at 60 °C. On 22 and 29 Oct 2012, we measured the population density, height, and crown size of the *P. densiflora* seedlings in Subplot B2.

Definition of index and calculation

To quantify the dynamic status of each subplot, we defined the index of dynamic status (IDS) by

$$IDS = \sum (yr \times \text{weight}), \quad (1)$$

where *yr* is a score given to the species. The score is equal to the year of the *i*th stage *Y(i)*. The stage is determined by the life-history traits of the species. Weight was defined as follows:

$$\text{weight} = v\text{-value} / (\sum v\text{-value}). \quad (2)$$

The *v*-value is a product of coverage and height of the species in the stand and correlated with the above-ground biomass (Sada et al. 1999, Yiruhan et al. 2001, Kobayashi et al. 2003, Kawada et al. 2005). The indices showed the weighted sum of *yr* of the constituent species so that larger values of the indices indicate later stages of succession.

We determined the *yr* scores based on Hayashi's (2003) stages of secondary succession. For example, we assigned a score of one to species with life-history traits that coincided with those of the first-stage species (dominant species in the first year). Similarly, we assigned scores of two, four, eight, 16, 32, and 64 to species with life-history traits that coincided with those of the second, third, fourth, fifth, sixth, and seventh stages, respectively (see *yr* in Table 1).

When we determined the stage that the concerned species belong to, we focused on the following life-history traits. Because the species of the first stage of an ideal succession is an annual herb that produces seed of the clitochore type, we focused on the life-history traits of annual herbs and the production of seeds of the clitochore type. Consequently, we classified species with life-history traits of annual herbs and the production of seeds of the clitochore type into species of the first stage of succession. Similarly, species that had life-history traits of biennial herbs and the production of seeds of the anemochore type were classified into the second stage of succession.

Species of the third and fourth stages are both perennial herbs, but those of the third stage have elongated rhizomes and those of the fourth stage form tussocks. Growth form tufts are strongly related with the life-history trait of making tussocks (Shimizu 2001). Consequently, we assigned species with perennial herbs and growth form tufts to the fourth stage. In Nemoto's study (2006), almost all species of the fourth stage consisted of species with growth form tufts and perennial herbs. Growth form tufts occurred mainly in Poaceae and Cyperaceae (Tsu-tida and Suganuma 1978, Shimizu 2001).

Salix bakko (dormancy form M: microphanerophyte; dwarf trees 3 – 8 m in height) belongs to the fifth stage (dominant in the 16th year) (Hayashi 2003), so that we assigned a score of 16 to *yr* of species with dormancy forms M and N (nanophanerophytes; shrubs 0.3 – 3 m in height). Similarly, we assigned a score of 32 to *yr* of species with dormancy form MM (mesophanerophytes; large trees > 8 m in height) and the life-history trait of production of seeds of the anemochore type, which belongs to the sixth stage. Furthermore, *Quercus mongolica* ssp. *crispula*, which produces seeds of the clitochore type belongs to the seventh stage, so we assigned a score of 64 to *yr* of species with dormancy form MM and the production of seeds of the clitochore type.

When we determined species life-history traits such as dormancy form, disseminule form, growth form, and flowering period, we referred to Numata and Yoshizawa (1975), Numata (1990), Osada (1993), Shimizu (1997), Asano (2005), and Hoshino and Masaki (2011). We referred to Miyawaki et al. (1994) for dormancy forms N, M, and MM. Some species have multiple growth forms (Numata 1957). Consequently, when we were not able to classify a species into a single stage, we assigned the score of the mean value between the corresponding two (e.g., if it was difficult to classify whether the score of a species was one or two, we gave 1.5).

RESULTS

The relation between *v*-value and above-ground dry weight of the herbs growing in the study area is approximated by

$$dw = 0.053 \times vv^{0.52}, \quad (3)$$

where *dw* is the above-ground dry weight (g) and *vv* is the *v*-value (cm³/m²) (ANOVA, $F_{1,4} = 6.116$, $P = 0.069$).

Species compositions and their *v*-values are shown in Table 1. In almost all subplots, the *v*-values of *M. sinen-*

Table 1. Species composition and v-value($10^7 \text{ cm}^3/\text{m}^3$). See text for yr.

Species	Study subplot													yr	
	A1	A2	A3	A4	B1	B2	C	D1	D2	D3	D4	E1	E2		E3
<i>Miscanthus sinensis</i>	681	2780	4682	6343	5375	9505	6609	2257	582	3383	4730	4610	12404	11846	8
<i>Spodiopogon sibiricus</i>		530	602	432	872	229	153	482	1009	1034	237	2481	1762	2461	8
<i>Pinus densiflora</i>						713					6149	12			32
<i>Artemisia princeps</i>	528	1380	1350	1888	350	100	128	64	199	690					4
<i>Sasa charitacea</i> var. <i>nana</i>					191	136	96	1415	689	978	140	193	245	969	16
<i>Eupatorium chinense</i> ssp. <i>sachalinense</i>	186	301	604	381	291	379	478	14	81	43	136				4
<i>Arundinella hirta</i>					100	109	394	1609	116	36	97			11	8
<i>Carex longerostrata</i> var. <i>pallida</i>	262	425	302	300	268	134	266	88	63	84	6				8
<i>Rhododendron japonicum</i>	207	42	233	129	57	574	50	21	46	59	447	38	141	99	16
<i>Smilax biflora</i> var. <i>trinervula</i>					266	16	382	19	230	38	306	565	54	265	4
<i>Thelypteris palustris</i>	12	60	51	34						44			1832		8
<i>Solidago virgaurea</i> var. <i>asiatica</i>	122	179	240	219	48	117	109	34	417	236	71	74			4
<i>Corylus heterophylla</i> var. <i>thunbergii</i>								165		236	1294				16
<i>Ligularia dentata</i>	268	463	532	263			10		1	4	144				4
<i>Lespedeza cyrtobotrya</i>					282		130	617	49		442				4
<i>Pteridium aquilinum</i> var. <i>latiusculum</i>	5	5	27	28	519	355	142	34			99				4
<i>Scabiosa japonica</i>					1	1		29	40		42	1094		2	1
<i>Osmunda claytoniana</i>	288	425	307	134											8
<i>Calamagrostis longiseta</i>									773	253					8
<i>Potentilla freyniana</i>	73	66	116	96	164	109	94	16	79	62	37	36		41	4
<i>Astilbe thunbergii</i> var. <i>formosa</i>	30	122	101	96	114	59	388								4
<i>Rubus microphyllus</i> var. <i>subcrataegifolius</i>	41	153	148	98	49	61	209		133		3		9		16
<i>Athyrium yokoscense</i>		26	23	13	63	5	328				125	11	250		8
<i>Sanguisorba longifolia</i>			162	110	67	28	81	49	111	35	48	65		20	4
<i>Brachypodium sylvaticum</i>	49	109	319	68		2	59		31						8
<i>Epipactis thunbergii</i>	194	145	94	17		62	38	12	4	21	22				4
<i>Carex caryophylla</i> var. <i>microtricha</i>													218	259	131
<i>Galium verum</i> var. <i>asiaticum</i> f. <i>nikkoense</i>	50	45	114	24	47	29	3	24	16	33	2	105	54	48	4
<i>Angelica pubescens</i>						408	100	68							4
<i>Allium thunbergii</i>	4	14	12	6	11	8		38		95	22	161	56	129	4
<i>Euphorbia pekinensis</i>	2	1		6	17	18	28	44	44	7	25	163	76	72	4
<i>Cirsium oligophyllum</i>		6	2	0	3	1		69		390	30				4
<i>Lycopus maackianus</i>					17		2		43	68				293	4
<i>Betula platyphylla</i> var. <i>japonica</i>					10	65			40	296					32
<i>Hydrangea paniculata</i>							383								16
<i>Geranium krameri</i>					50	32				21		134	87	35	4
<i>Malus toringo</i>					228	31					59	43			16
<i>Geranium yesoense</i> var. <i>nipponicum</i>	3	3		19	7	1	14	42	113	72	72				4
<i>Patrinia scabiosaeifolia</i>							2	75		145	27	91			4

<i>Anaphalis margaritacea</i>												65	12	137	73	46						4
<i>Erigeron strigosus</i>																						2
<i>Iris ensata</i> var. <i>spontanea</i>	29	66	56	75					14	20	4	37	25	4	32	174	36	26	18			8
<i>Ixeris dentata</i>	2	8							61		48	58	25	48	24	34	40		10			4
<i>Carex humilis</i>											88	4	41	88	4	31	166					4
<i>Cirsium japonicum</i>	7		4	5	4				40	43	72		43	72	63	10						4
<i>Populus sieboldii</i>																	169					4
<i>Carex oxyandra</i>	10	25	12	62	3	3			3	60	3	3	60	3	12	1	11	38				32
<i>Angelica decursiva</i>	12	32	57	9	4	18			4	4	25	4	4	25	32	16	22					8
<i>Aster ageratoides</i> ssp. <i>ovatus</i>	17	20	22	22	115				4	4	11											4
<i>Disporum smilacinum</i>	21	8	6	12	1	90			54	13												4
<i>Moehringia lateriflora</i>	27	27	35	36	5	2			4	2	3											4
<i>Gentiana scabra</i> var. <i>buengeri</i>	3	9	47	9	9	16			16	3												4
<i>Quercus mongolica</i> ssp. <i>crispula</i>																	202					64
<i>Lysimachia vulgaris</i> var. <i>davurica</i>	28	47	59	42						18												4
<i>Adenophora triphylla</i> var. <i>japonica</i>	5	11	5	2	10	6			10	6	29				7					117		4
<i>Bistorta major</i> var. <i>japonica</i>	41	70	50	9	15																	4
<i>Viola patrinii</i>	5	7	9	16						59	9					4	8	4	24	37		4
<i>Senecio cannabifolius</i>	9	14	19	19	113																	4
<i>Celastrus orbiculatus</i> var. <i>papillosus</i>																	5	103				16
<i>Lonicera morrowii</i>																						16
<i>Eupatorium lindleyanum</i>																	62	4		18		4
<i>Aster scaber</i>																	40					4
<i>Polygonatum odoratum</i> var. <i>pluriflorum</i>	23	3	6		12	7									5	17	12			64		4
<i>Dianthus superbus</i>	1	6	5	3						9	2				36			58			25	4
<i>Viola hirtipes</i>	7	14	20	26	17	18			35	3								1		4		4
<i>Reynoutria japonica</i>	9	30	29	22	10	18			6						17							4
<i>Lysimachia clethroides</i>	14				21	78			22													4
<i>Senecio flammeus</i> var. <i>glabrifolius</i>	3	8	13	13	50	16			2	21							7					4
<i>Symplocos chinensis</i> var. <i>leucocarpa</i> f. <i>pilosa</i>																						4
<i>Hosta sieboldii</i> f. <i>lancifolia</i>	4	6	12	9	1	18				7	18							11	8		132	16
<i>Seseli libanotis</i> ssp. <i>japonica</i>	47	24	41							10												4
<i>Hypericum erectum</i>	3	5	6							4	1				7	10	5	6	35		39	4
<i>Senecio nemorensis</i>											34				13	70						4
<i>Hemerocallis vespertina</i>																		84	24			4
<i>Chaenomeles japonica</i>																					105	4
<i>Lespedeza cuneata</i>																		51			43	4
<i>Campanula punctata</i> var. <i>hondoensis</i>	12	10		16	18	6			4	11												4
<i>Thalictrum aquilegifolium</i> var. <i>sibiricum</i>		10	38	9	11	7										5					6	4
<i>Thalictrum aquilegifolium</i> var. <i>intermedium</i>	40	21		4	19																	4
<i>Potentilla fragarioides</i> var. <i>major</i>	7	15	9	7	4				19	15												4
<i>Phragmites australis</i>																					80	8

Table 1. Continued

Species	Study subplot													Y*		
	A1	A2	A3	A4	B1	B2	C	D1	D2	D3	D4	E1	E2		E3	
<i>Silene firma</i>		23	55					2								1
<i>Pseudolysimachion rotundum</i> var. <i>subintegrum</i> f. <i>petiolatum</i>													79			4
<i>Artemisia japonica</i> f. <i>laciniifolia</i>									79							4
<i>Pseudolysimachion rotundum</i> var. <i>subintegrum</i>							6			53		9	8			4
<i>Trisetum sibiricum</i>																4
<i>Aconitum japonicum</i> ssp. <i>maritimum</i>									68							4
<i>Achillea alpina</i> var. <i>discoidea</i>					23	19	9	2	2	13						4
<i>Muhlenbergia japonica</i>				6					57							8
<i>Polygonatum humile</i>	6	9	16	17	2		1	1	1	9						4
<i>Calamagrostis arundinacea</i> var. <i>brachytricha</i>				17	43											8
<i>Picris hieracioides</i> var. <i>glabrescens</i>	1	2		0	12	8	4	2	24							2
<i>Platycodon grandiflorum</i>												52				4
<i>Synurus excelsus</i>	1	1	2	2	8		8	8	16	12						4
<i>Serratula coronata</i> ssp. <i>insularis</i>							6	6	44							4
<i>Pedicularis resupinata</i> var. <i>oppositifolia</i>							24	24			23					4
<i>Anracylodes japonica</i>							29	29	13	4						4
<i>Viola rossii</i>							16	16	29							4
<i>Hieracium umbellatum</i>							19	19							20	4
<i>Silene firma</i> f. <i>pubescens</i>				33			4	4								1
<i>Saussurea maximowiczii</i>							36	36								4
<i>Oenothera biennis</i>		0	2	5	14	2	1	0			8	2				1
<i>Hemerocallis middendorffii</i> var. <i>esculenta</i>	2	1									29					4
<i>Halenia corniculata</i>							32	32								1
<i>Melampyrum laxum</i> var. <i>nikkoense</i>							11	11			20					1.5
<i>Carex blepharicarpa</i>									29							8
<i>Salix bakko</i>											28					16
<i>Veratrum maackii</i> var. <i>reymondianum</i>	1	1				25										4
<i>Achillea alpina</i>							6	6		21						4
<i>Prunella vulgaris</i> ssp. <i>asiatica</i>	1	7	3	2			4	5	3			2				4
<i>Calamagrostis langsdorffii</i>								26								4
<i>Agrostis clavata</i>	1	9	10	5												8
<i>Ajuga shikotanensis</i> f. <i>hirsuta</i>						2			22							4
<i>Viola pumilio</i>					5	5	0	0	7	5	1					4
<i>Cirsium dipsacolepis</i>							13	13		7						4
<i>Saussurea tanakae</i>							20	20								4
<i>Stenactis annuus</i>	3	9	2			5										2

<i>Lilium leichtlinii</i> var. <i>tigrinum</i>	3	1	4	10	4									
<i>Saussurea pulchella</i>			17		2									
<i>Artemisia japonica</i>			17		4									
<i>Veronicastrum japonicum</i>	3	7	7		4									
<i>Luzula multiflora</i>	8	6			4									
<i>Saussurea ussuriensis</i>			13		4									
<i>Rhamnus japonica</i> var. <i>deciptens</i>				13	16									
<i>Parnassia palustris</i> var. <i>multisetata</i>	0	2	4	2	4									
<i>Hierochloa bungeana</i>				5	7									
<i>Hosta montana</i>		1	5	4	4									
<i>Festuca ovina</i>			5	6	8									
<i>Lycopodium clavatum</i>				8	8									
<i>Rosa multiflora</i>				7	16									
<i>Polygala japonica</i>			4		4									
<i>Thalictrum minus</i> var. <i>hypoleucum</i>			2		4									
<i>Ranunculus japonicus</i> var. <i>akagiensis</i>	1	3			4									
<i>Platanthera tipuloides</i>		2			4									
<i>Helionopsis orientalis</i>				2	4									
<i>Glycine max</i> ssp. <i>soja</i>		3			1									
<i>Polygonatum falcatum</i>	8		3		4									
<i>Amphicarpaea bracteata</i> ssp. <i>edgeworthii</i> var. <i>japonica</i>		1	1	1	1									
<i>Euonymus sieboldianus</i> var. <i>sanguineus</i>				3	16									
<i>Aster glehnii</i> var. <i>hondoensis</i>		2			4									
<i>Rabdosia inflexa</i>			2		4									
<i>Clinopodium chinense</i> var. <i>parviflorum</i>			2		4									
<i>Viola acuminata</i>			2		4									
<i>Taraxacum</i> sp.				2	4									
<i>Codonopsis ussuriensis</i>				2	4									
<i>Geranium thunbergii</i>		2			4									
<i>Euphrasia maximowiczii</i>				2	1.5									
<i>Pogonia minor</i>			2		4									
<i>Botrychium ternatum</i>					4									
<i>Ligularia stenocephala</i>		1	1	1	4									
<i>Larix kaempferi</i>				1	32									
<i>Patrinia triloba</i>			1		4									
<i>Pyrola nephrophylla</i>				1	4									
<i>Luzula plumosa</i> var. <i>macrocarpa</i>			1		8									
Total <i>v</i> -value	3445	7892	10705	11233	10287	13758	10904	7117	7060	9358	15525	10686	17858	16941

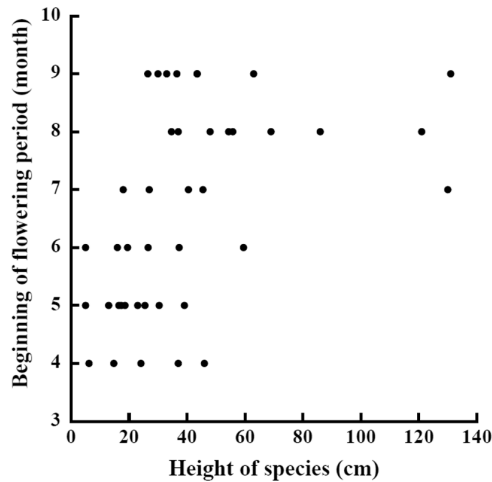


Fig. 1. Relation between the beginning of the flowering period and the height of the species in Subplot D4.

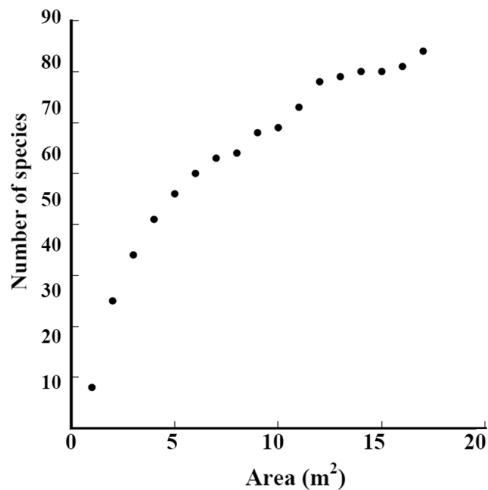


Fig. 2. Species-area curve in Subplot D1

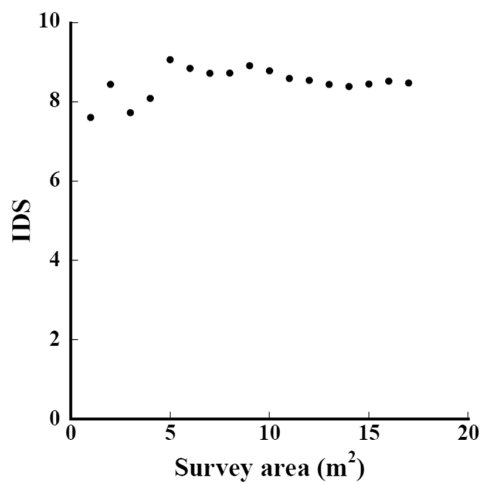


Fig. 3. Relation between indices and survey area in Subplot D1.

sis were the largest among the constituent species. The sum of the ν -values of constituent species in Subplots A1, A2, A3, and A4 gradually increased. The relation between the beginning of the flowering period and the height of species in Subplot D4 is shown in Fig. 1. We were able to divide the species into two groups: Group 1 contained earlier flowering and smaller height species and Group 2 contained later flowering and taller species. Smaller species tended to flower before the elongation of taller species.

The species-area curve of Subplot D1 is shown in Fig. 2. The total number of species continued increasing in the 17 m² area. We should survey a wider area to record all growing species.

The relation between the indices and survey area in Subplot D1 is shown in Fig. 3. When the survey area was 17 m², the IDS was 8.5. Even when the survey area was 1 m², the IDS was within $\pm 10\%$ of the value 8.5. Furthermore, when the survey area exceeded 6 m² and 11 m², IDS converged was within $\pm 5\%$ and $\pm 1\%$, respectively. The IDS converges into a value at smaller areas than the area needed when the number of species converges.

The IDS in Subplot A1 was 6.4, Subplot A2 was 6.5, Subplot A3 was 6.8, and Subplot A4 was 6.9. We conducted vegetation surveys in Subplot A1 2 months after the prescribed burning, in Subplot A2 3 months after burning, in Subplot A3 4 months after burning, and in Subplot A4 5 months after burning. The indices gradually increased in the growing season. The indices were 7.5 in Subplot B1 and 7.6 in Study plot C. We conducted vegetation surveys in Subplots B1 4 years after prescribed burning and in Study plot C 3 years after burning. The indices were larger than those of plots within a year after the prescribed burning. The IDS of Subplot B2 was 9.2. The IDS was 8.5 in Subplot D1, 7.8 in Subplot D2, 9.7 in Subplot D3, and 18.5 in Subplot D4. The IDS was 6.9 in Subplot E1, 8.1 in Subplot E2, and 8.2 in Subplot E3.

The relation between the sum of the ν -values of the trees and the IDS was approximated by

$$IDS_t = 0.000014 \times \nu\text{-value}_t + 6.5272, \quad (4)$$

where IDS_t is the IDS of the subplots in this study and $\nu\text{-value}_t$ is the sum of the ν -values (cm³/m²) in each subplot (Fig. 4). (ANOVA, $F_{1,12}=601$, $P = 1.3 \times 10^{-11}$, $R^2=0.9824$). The indices were significantly correlated with the ν -value of the trees.

The relation between the ν -values of dwarf bamboo (*Sasa chartacea* var. *nana*) and those of trees other than dwarf bamboo is shown in Fig. 5. The trees other than dwarf bamboo did not grow in the place where dwarf

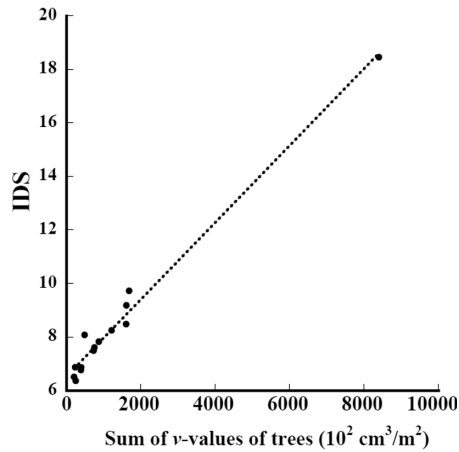


Fig. 4. Relation between the sum of v -values of trees and indices.

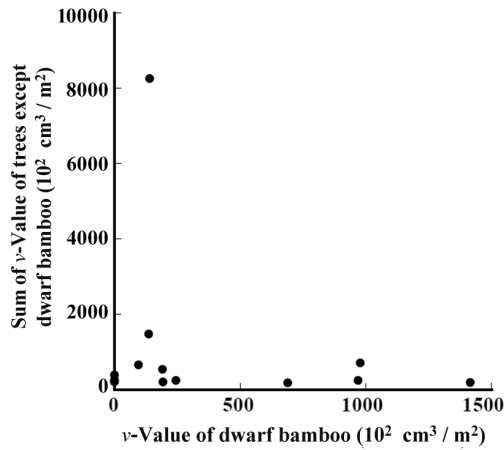


Fig. 5. Relation between the v -value of dwarf bamboo and the summed v -value of trees other than dwarf bamboo.

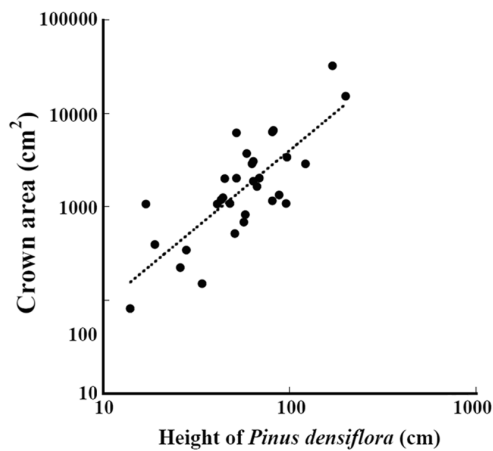


Fig. 6. Relation between the height of *Pinus densiflora* seedlings and their crown area.

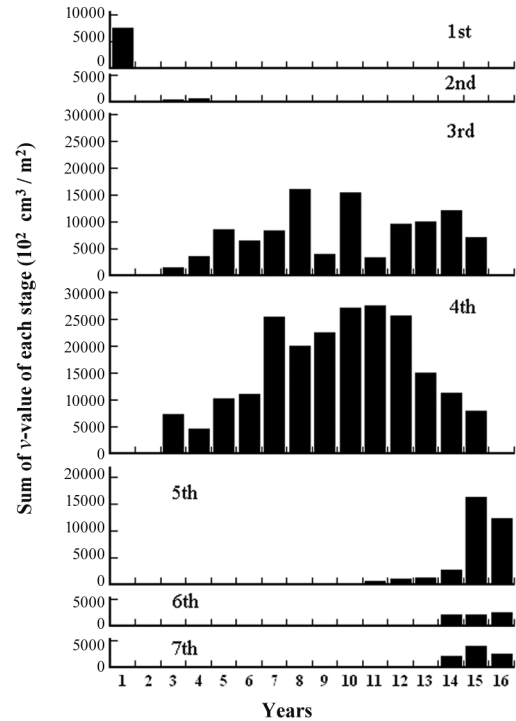


Fig. 7. Alternation of stages and the v -value of their species

bamboo grew. Among the percentages of v -value of trees other than dwarf bamboo, larger values were that of *P. densiflora* (33%) and *Rhododendron japonicum* (22%).

The relation between the height of *P. densiflora* seedlings and their crown area was approximated by

$$\text{crown_a} = 2.00 \times \text{height_p}^{1.65}, \quad (5)$$

where crown_a is the crown area (cm^2) and height_p is the height (cm) (Fig. 6) (ANOVA, $F_{1,29}=11.5$, $P = 0.0019$). The crown area was significantly correlated with the height.

The number of *P. densiflora* seedlings growing in a 30-m^2 area was 13 (0.43 individual / m^2).

DISCUSSION

Iijima and Sado (2005) conducted experiments on secondary succession for 16 years after they denuded the area. We calculated the v -values of the constituent species and indices using data on height and coverage in their report. The dominant species subsequently changed (Fig.7). The relation between the years since they denuded the area and the indices was approximated by

$$\text{IDS}_i = 0.96 \times \text{year_L} + 0.355, \quad (6)$$

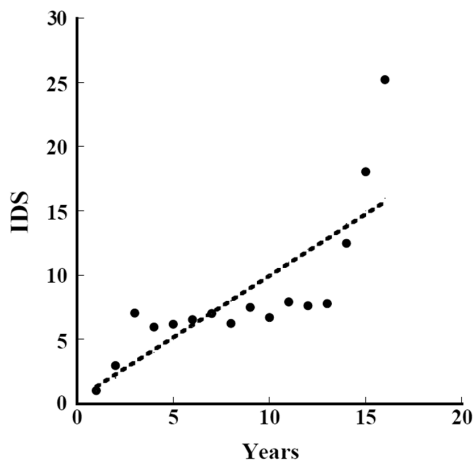


Fig. 8. Relation between years since the denudation of the area and indices.

where IDS_i is the value of the IDS by Iijima and Sago's data and $year_L$ is the years since they started the experiment from the denuded area (Fig. 8) (ANOVA, $F_{1,14}=22.97$, $P = 0.000286$). The indices were significantly correlated with the length of years in secondary succession since they denuded the area. The increment of change in the IDS per year was 0.96.

According to Prach (1990), *Glechoma hederacea*, a Lamiaceae perennial herb with long, aerial runners or stolons (Birch and Hutchings 1999), became dominant at about the fifth year in the mesic sere of Bohemia, Czech. Furthermore, he reported that *Arrhenatherum elatius*, a tussock-forming Poaceae perennial species (Pfitzenmeyer 1962), became dominant at about the 15th year and that *Prunus spinosa*, a European shrub, became dominant at about the 25th year. Dölle et al. (2008) reported that the stages of annual herbs, perennial grasslands, shrubs, and pioneer forests were the periods of 1st-2nd years, 3rd-8th years, 10th-14th years, and after about 20 years of succession up to now, respectively, in Germany. Collins and Adams (1983) reported that in the area where they plowed once, the percentage coverage of forbs and grasses peaked in the first and tenth years in Oklahoma. We need modifications in years and categories to apply the IDS to other areas.

Kawakami et al. (personal communication) conducted vegetation surveys for 4 years between 2008 and 2011 in the same study area as ours and set a total of 179 1 m × 1 m quadrats. We calculated indices using their data of height and coverage. The relation between the length of years of restoration since the prescribed burning and the indices of their study and ours was approximated by

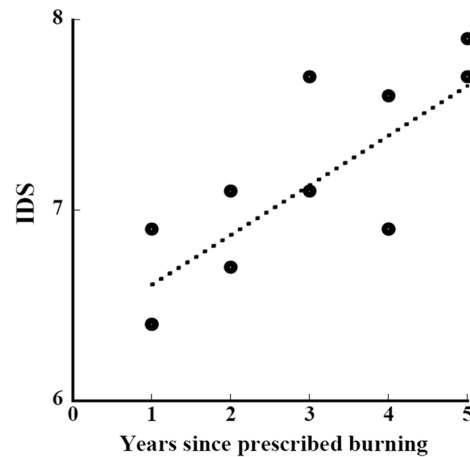


Fig. 9. Relation between the number of years of restoration since the prescribed burning and the indices of their study and ours.

$$IDS_b = 0.2612 \times year_b + 6.3465, \quad (7)$$

where IDS_b is the IDS of the subplot and $year_b$ is the years since the prescribed burning of the subplot (Fig. 9) (ANOVA, $F_{1,10}=14.54$, $P=0.0034$). The indices were significantly correlated with the length of years of restoration. The increment of the IDS in a year during the restoration period since the prescribed burning was 0.26. The increment of 0.26 per year is as small as one-fourth of the aforementioned increment of 0.96 in succession without disturbance.

R. japonicum was able to sprout when its above-ground shoot was damaged (Nakano and Tsutida 2004). However, *P. densiflora* was not able to sprout once its above-ground shoot was damaged (Kato, personal communication). Therefore, when *P. densiflora* is damaged, it takes a few years to achieve seed dispersal, germination, and growth before it is renewed. Depletion of the sprouting ability in *P. densiflora* accounts for the slow restoration speed when prescribed burning in the grasslands was performed.

According to the reports of Negishi and Yagi (1985), Wu and Ando (2008), and Ogura (2009), the relation between the age and the height of the initial growing stage of *P. densiflora* is approximated by

$$height_{pd} = 3.43 \times y_p^{1.81}, \quad (8)$$

where $height_{pd}$ is the height (cm) of *P. densiflora* in y_p years after germination (ANOVA, $F_{1,13} = 18.3$, $P = 0.00090$).

Because they conducted tree cutting in Subplot B2 in autumn 2008, the ages of *P. densiflora* seedlings growing in Subplot B2 were between 1 and 4 years old. Consequently, the mean number of *P. densiflora* seedlings were 3.25 individuals per year per 30 m² (0.11 individual m⁻² year⁻¹).

Using Equations (5) and (8), we were able to estimate the volume, the product of the crown area and the height, of *P. densiflora* seedlings using the following equation:

$$vv_a = 52.41 \times y_p^{4.80}, \quad (9)$$

where vv_a is the volume (cm^3) of *P. densiflora* in y_p years after germination.

Furthermore, with a mean annual establishment rate, 0.11 individuals $\text{m}^{-2} \text{year}^{-1}$, we were able to estimate the increment of v -value of *P. densiflora* seedlings by

$$\Delta vv = 5.76 \times y_p^{4.80}, \quad (10)$$

where Δvv is the increment of v -value of *P. densiflora* seedlings in a 1 m \times 1 m quadrat per year in y_p years after germination ($\text{cm}^3 \text{m}^{-2} \text{year}^{-1}$).

Of the 14 subplots, the mean of the sum of v -values other than for *P. densiflora* was $1042100 \text{ cm}^3 / \text{m}^2$ ($\text{SD}=3775 \text{ cm}^3 / \text{m}^2$, $N=14$). Therefore, the contribution by *P. densiflora* seedlings to the IDS in n years after germination is estimated by

$$\Delta \text{IDS}(n) = 32 \times \left\{ \left(\sum_{y,p=1}^n \Delta vv \right) / (1042100 + \sum_{y,p=1}^n \Delta vv) \right\}, \quad (11)$$

where, $\Delta \text{IDS}(n)$ is the contribution by *P. densiflora* seedlings to the IDS in n years after germination and Δvv is defined in Equation (10).

With Equations (10) and (11), we were able to estimate ΔIDS (5), which is the contribution by *P. densiflora* seedlings to the IDS 5 years after germination, as 0.54 (0.11 / year). Consequently, of the aforementioned annual increment of 0.26 in the IDS during the restoration period since prescribed burning, 0.11 (42%) was contributed by *P. densiflora* seedlings.

CONCLUSION

We estimated the IDS of grasslands with the coverage and height of constituent species. Using the IDS, we quantitatively analyzed the effect of the disturbance of prescribed burning. Trees are affected by the disturbance of prescribed burning. We calculated, using the annual establishment and growth rates, the contribution by *P. densiflora* to restoration following the prescribed burning.

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