

Which Genus to Study? In Search of Plant Genera Underrepresented or Overrepresented in the Research from the Flora of Japan

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Abstract One good criterion for determining certain plant groups as a research target would be to choose those much less or much more studied than the average. Here I conducted a brief survey on research effort already made for each of the 84 angiosperm genera, in which 10 or more species are recorded as native to Japan. For each of the genera, approximate amount of the research effort was measured by counting the number of literature titles and the number of nucleotide sequences available online. I found a clear tendency that the amount of research effort strongly correlates with the generic size (the number of species in the world for a given genus). Judging from the deviation from this tendency, I found that four genera were exceptionally well studied and 14 genera were relatively less studied despite their generic size. I propose the statistics presented here would be one of the good criteria for starting new research projects on the flora of Japan, which is facing serious loss of diversity largely because of human activities.

Key words: endemic species, flora of Japan, genus, research effort, species richness.

Introduction

The Japanese Archipelago harbors remarkably rich and unique flora in its relatively small land area (Iwatsuki, 1995) and thus has been serving as a valuable field for plant biology including community-level studies on pollination (Kato *et al.*, 1990, 1993 and 2003; Kato, 2000), seed dispersal (Noma and Yumoto, 1997), phytogeography (Fujii *et al.*, 2002; Fujii and Senni, 2006; Aoki *et al.*, 2004; Ikeda *et al.*, 2006; Ikeda and Setoguchi, 2006, 2007), and developmental anatomy (Takahashi, 1994; Ota *et al.*, 2001; Tobe, 2008) and molecular systematics (Nakazawa *et al.*, 1997; Okuyama *et al.*, 2005, 2008; Yamaji *et al.*, 2007) using endemic species. Despite the considerable number of studies conducted, however, much of the natural history of the plants native to Japan remains yet to be studied. Meanwhile, comprehensive field collection of any data on plants native to Japan is becoming

more and more difficult, with more than a quarter of species now being considered endangered of extinction largely because of human activities (Environment Agency of Japan, 2000) and increasing deer browsing (Kato and Okuyama, 2004). Therefore, some guidelines for establishment of efficient strategies on researches, which utilize the vast diversity of plants native to Japan, are needed. To this end, the overall picture on how our knowledge of natural history in the flora of Japan is distributed is crucial, although it has not been clearly presented yet.

In this study, I aimed to reveal the general patterns on the research effort made for each of the angiosperm genera native to Japan. I expect the genus with more constituent species is likely to have more topics to be studied. If this is true, there should be a tendency that larger genera have more research efforts made. In turn, plant genera that have relatively fewer publications despite their size might have more important

findings to be revealed, while those with more publications would serve as model systems for studies on plant diversity in Japan.

Here, I surveyed the publication records regarding the 84 genera of Japan, which have 10 or more native species. Specifically, I addressed the following questions: (1) First, which genus is especially species rich in Japan compared to other regions? (2) Second, among the plant genera, is there a correlation between the number of constituent species and research effort made? (3) Third, if the correlation is present, which genera are overly represented and which are underrepresented in literature in proportion to their species richness? (4) And finally, which genera should we prioritize to work on?

Materials and Methods

Data collection

With the aid of the Wild Flora of Japan (Satake *et al.*, 1981, 1989), I selected 84 flowering plant genera in which the number of species native to Japan exceeds 10. Hereafter I refer to these 84 genera as “species-rich angiosperm genera of Japan”. Note that this number of genera might be slightly an underestimate, as the Wild Flora of Japan does not include herbaceous plants in Ryukyu Islands. Next, I coded the number of species native to Japan and the number of endemic species in Japan based on the number of species listed in the Wild Flora of Japan (Satake *et al.*, 1981, 1989), and supplemented the information with Flora of Japan (Iwatsuki *et al.*, 1993; 1995, 1999, 2001 and 2006) where possible. In addition, the worldwide number of species for each of the genera was also coded based on The Plant-Book (Mabberley, 1997).

To measure the amount of research effort made for each genus, two measures were used, i.e., number of literature titles and the number of nucleotide sequences each available online. The approximate number of literature titles regarding each of the 84 genera was retrieved using Google Scholar (<http://scholar.google.co.jp/>) by entering the two words “genus ‘name’” with quotation

symbols into the form (e.g., for genus *Acer*, “genus *Acer*” were used as a key) on December 2, 2009. This should result in the underestimate of the number of literature titles retrieved, as genus names are not always coupled with the word “genus”, but apparently could prevent the erroneous inflation of the number due to occasional, multiple meanings of the genus name. Likewise, the number of nucleotide sequences deposited online were count using the query form of the nucleotide database of National Center for Biotechnology Information (NCBI) website (<http://www.ncbi.nlm.nih.gov/>). The full taxonomy path was used as a query to enter into the form to minimize the erroneous hit (e.g., for genus *Acer*, “Eukaryota; Viridiplantae; Streptophyta; Embryophyta; Tracheophyta; Spermatophyta; Magnoliophyta; eudicotyledons; core eudicotyledons; rosids; eurosids II; Sapindales; Sapindaceae; *Acer*” was used as a query.)

Data analysis

The relative species richness and the relative endemism in Japan were calculated by dividing the number of native/endemic species in Japan by the number of species in the world for each of the 84 genera. These values are expected to be high for genera having Japan as their center of diversity, making them suitable for screening candidate plant lineage for pursuing research in Japan as a valuable research field.

The presence of significant correlation between the overall number of species and the number of literature titles available online, and between the overall number of species and the number of nucleotide sequences deposited online, for each of the 84 genera, was tested using Spearman’s rank correlation test. Furthermore, linear regression of the number of literature titles or the number of nucleotide sequences deposited online using the overall number of species for the genus as an explanatory variable was also conducted, and 50% and 95% expectation interval was also arbitrary set and calculated based on the regression in order to find out “outlier” genera in terms of research effort. All statistical analyses in this

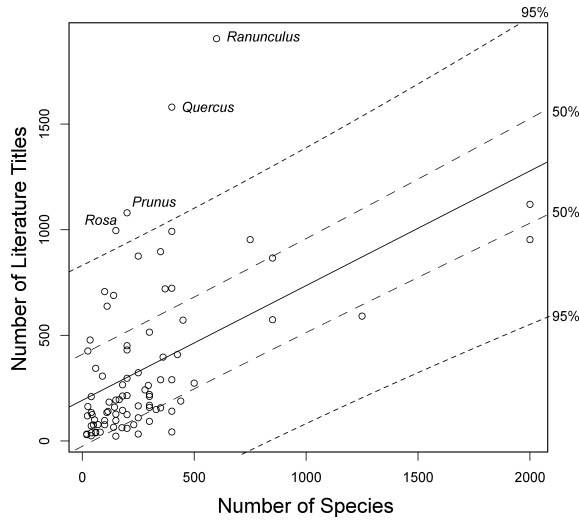


Fig. 1. The relationship between the number of species and the number of literature titles available online for 84 species-rich angiosperm genera of Japan. The solid line indicates the regression line best goodness-of-fit according to the Spearman's rank-correlation test ($y=0.5428x+192.6$). 50% and 95% confidence interval from the regression are also shown with broken lines.

study were made using the statistical program R ver. 2.9.1 (R Development Core Team, 2009).

Results

All the measures surveyed in the present study are listed in Table 1. Both the relative species richness and the relative endemic richness in Japan were found to be highest in the following five genera, i.e., *Hosta* (Agavaceae), *Tricyrtis* (Ruscaceae), *Asarum* (Aristolochiaceae), *Hydrangea* (Hydrangeaceae), and *Mitella* (Saxifragaceae) (Table 1, shown in bold), indicating that these genera have their center of diversity in Japan.

Figure 1 shows the scatter plot between the number of species in the world and the number of literature titles available online for the 84 species-rich angiosperm genera of Japan. As expected, the number of literature titles was positively correlated with the number of species in the world (Spearman's rank correlation, $P < 5.0 \times 10^{-7}$, $\rho = 0.53$), indicating the research effort for each genus is somewhat proportional to its size. The outlier genera in terms of research

effort proportional to the generic size were only found as those with the number of literature titles exceeding the 95% credibility threshold as expected from the regression ($y = 0.5428x + 192.6$). These outlier genera found were *Ranunculus* (Ranunculaceae), *Quercus* (Fagaceae), *Prunus* (Rosaceae), and *Rosa* (Rosaceae). By placing 50% threshold, more genera were found as the outliers, in which the number of literature titles either exceed or fall below the number expected from the regression. Under this criterion, 14 genera, i.e., *Calanthe* (Orchidaceae), *Fimbristylis* (Cyperaceae), *Eriocaulon* (Eriocaulaceae), *Stellaria* (Caryophyllaceae), *Euonymus* (Celastraceae), *Calamagrostis* (Poaceae), *Saussurea* (Asteraceae), *Symplocos* (Symplocaceae), *Corydalis* (Fumariaceae), *Thalictrum* (Ranunculaceae), *Pedicularis* (Orobanchaceae), *Saxifraga* (Saxifragaceae), *Senecio* (Asteraceae), and *Euphorbia* (Euphorbiaceae), were found to have especially fewer publications online than expected from the regression.

As shown in Fig. 2, the number of nucleotide sequences deposited online for each genus also positively correlated with its number of species

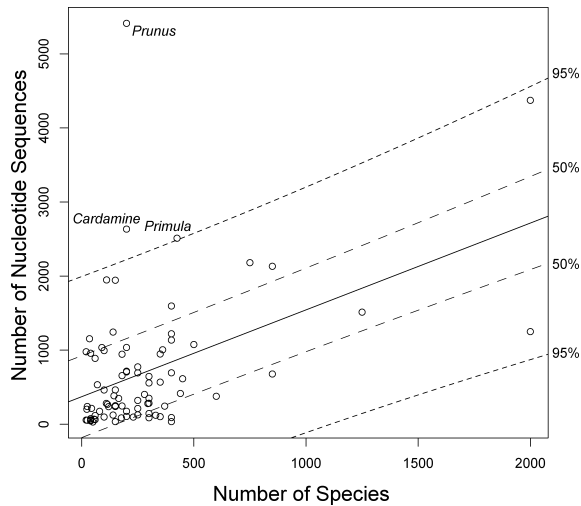


Fig. 2. The relationship between the number of species and the number of nucleotide sequences deposited in GenBank for 84 species-rich angiosperm genera of Japan. The regression lines are also shown as in Fig. 1 ($y=1.172x+371.4$).

in the world, but the tendency was weaker (Spearman's rank correlation, $P < 5.0 \times 10^{-4}$, $\rho = 0.40$). Again, the outlier genera found were only those exceeding the number expected from the regression ($y=1.172x+371.4$) if I put 95% threshold. These were *Prunus* (Rosaceae), *Cardamine* (Brassicaceae), and *Primula* (Primulaceae). Like in the number of literature titles, more genera were found as the outliers, for which the number of nucleotide sequences are either exceeding or below the number expected from the regression by placing 50% threshold.

Discussion

Before determining certain plant groups to study, it would be good to know which is relatively less studied, and which is relatively more so. I presented here a first attempt for quantifying the amount of research effort already made for individual genera. Although one can start a research project on plant natural history in various points of view, including that focuses on populations, species or higher taxa, or communities, it is good to keep in mind that one of the most remarkable methodological progresses on plant biology in the last decades is the wide-

spread and routine use of molecular phylogenetics (Savolainen and Chase, 2003). In light of phylogenetic information, regardless of that of populations or species, one can conduct comparative studies on any traits of interest, especially in association with the other factors (Martins and Hansen, 1997). This will result in a deeper understanding of the origins and adaptive functions of diverse characteristics of the focal plants. To this end, it would be a good research strategy to focus on certain lineages of plants such as genera, especially those having many, say 10 or more, species native to Japan. Therefore, in this study, I only included the angiosperm genera with 10 or more species native to Japan in the analyses.

As a result, I revealed that there is a general, clear trend that more effort tends to be paid to genera with more species. Although this finding itself might not be so surprising, one can see if a certain genus has a deviation from this general trend. To quantify this deviation, here I propose literature collection index (LCI) and nucleotide collection index (NCI), where each of the measure is calculated from the number of literature titles/nucleotide sequences deposited online for a certain genus divided by that expected from the

Table 1. A summary of species richness, endemism, and research effort made for 84 species-rich angiosperm genera of Japan

Family	Genus	No. of species in the world	No. of native species in Japan	No. of endemic species in Japan	Nucleotide sequences on web	Literature titles on web	Relative species richness in Japan (%)	Relative endemic richness in Japan (%)	LCI ^a	NCI ^b
POTAMOGETACEAE	<i>Potamogeton</i>	90	14	0	1035	307	15.6	0.0	1.27	2.17
AGAVACEAE	<i>Hosta</i>	25	12	11	54	163	48.0	44.0	0.79	0.13
LILIACEAE	<i>Lilium</i>	100	13	7	994	707	13.0	7.0	2.86	2.03
RUSCACEAE	<i>Polygonatum</i>	55	12	4	68	100	21.8	7.3	0.45	0.16
	<i>Tricyrtis</i>	20	11	10	56	30	55.0	50.0	0.15	0.14
DIOSCOREACEAE	<i>Dioscorea</i>	850	11	5	678	574	1.3	0.6	0.88	0.50
JUNCACEAE	<i>Juncus</i>	300	27	3	350	159	9.0	1.0	0.45	0.48
	<i>Luzula</i>	115	11	1	268	140	9.6	0.9	0.55	0.53
ERIOCAULACEAE	<i>Eriocaulon</i>	400	35	25	35	43	8.8	6.3	0.10	0.04
POACEAE	<i>Calamagrostis</i>	230	17	10	96	77	7.4	4.3	0.24	0.15
	<i>Poa</i>	200	17	8	706	431	8.5	4.0	1.43	1.17
ARACEAE	<i>Arisaema</i>	150	25	21	250	127	16.7	14.0	0.46	0.46
CYPERACEAE	<i>Carex</i>	2000	252	93	4373	1120	12.6	4.7	0.88	1.61
	<i>Cyperus</i>	300	26	2	144	220	8.7	0.7	0.62	0.20
	<i>Eleocharis</i>	120	15	1	237	184	12.5	0.8	0.71	0.46
	<i>Fimbristylis</i>	250	18	2	126	33	7.2	0.8	0.10	0.19
	<i>Scirpus</i>	200	24	5	105	215	12.0	2.5	0.71	0.17
ORCHIDACEAE	<i>Calanthe</i>	150	15	7	35	23	10.0	4.7	0.08	0.06
	<i>Cymbidium</i>	44	10	5	214	125	22.7	11.4	0.58	0.51
	<i>Liparis</i>	350	10	1	102	290	2.9	0.3	0.76	0.13
	<i>Platanthera</i>	40	17	7	50	72	42.5	17.5	0.34	0.12
SALICACEAE	<i>Salix</i>	400	29	8	694	992	7.3	2.0	2.42	0.83
BETULACEAE	<i>Alnus</i>	25	11	6	239	426	44.0	24.0	2.07	0.60
	<i>Betula</i>	35	11	7	1154	478	31.4	20.0	2.26	2.80
FAGACEAE	<i>Quercus</i>	400	15	2	1596	1580	3.8	0.5	3.86	1.90
URTICACEAE	<i>Boehmeria</i>	80	18	8	174	42	22.5	10.0	0.18	0.37
MORACEAE	<i>Ficus</i>	750	16	3	2181	953	2.1	0.4	1.59	1.74
POLYGONACEAE	<i>Polygonum s. l.</i>	200	39	0	1036	451	19.5	0.0	1.50	1.71
	<i>Rumex</i>	200	10	1	716	297	5.0	0.5	0.99	1.18
CARYOPHYLLACEAE	<i>Stellaria</i>	200	18	3	175	60	9.0	1.5	0.20	0.29
RANUNCULACEAE	<i>Aconitum</i>	300	24	17	283	515	8.0	5.7	1.45	0.39
	<i>Anemone</i>	144	13	3	384	160	9.0	2.1	0.59	0.71
	<i>Clematis</i>	295	25	12	279	263	8.5	4.1	0.75	0.39
	<i>Ranunculus</i>	600	25	6	377	1904	4.2	1.0	3.67	0.35
	<i>Thalictrum</i>	330	17	5	121	149	5.2	1.5	0.40	0.16

Table 1. (Continued)

Family	Genus	No. of species in the world	No. of native species in Japan	No. of endemic species in Japan	Nucleotide sequences on web	Literature titles on web	Relative species richness in Japan (%)	Relative endemic richness in Japan (%)	LCI ^a	NCI ^b
ARISTOLOCHIACEAE	<i>Asarum</i>	70	50	47	533	78	71.4	67.1	0.34	1.18
CLUCIACEAE	<i>Hypericum</i>	370	35	29	244	720	9.5	7.8	1.83	0.30
PAPAVRACEAE	<i>Corydalis</i>	400	15	3	90	141	3.8	0.8	0.34	0.11
BRASSICACEAE	<i>Cardamine</i>	200	15	4	2634	125	7.5	2.0	0.42	4.35
CRASSULACEAE	<i>Sedum</i>	280	17	9	402	242	6.1	3.2	0.70	0.57
HYDRANGEACEAE	<i>Hydrangea</i>	23	12	8	202	119	52.2	34.8	0.58	0.51
SAXIFRAGACEAE	<i>Chrysosplenium</i>	60	18	11	62	39	30.0	18.3	0.17	0.14
	<i>Mitella</i>	20	11	10	978	33	55.0	50.0	0.16	2.48
	<i>Saxifraga</i>	440	16	6	415	189	3.6	1.4	0.44	0.47
	<i>Potentilla</i>	500	23	2	1076	274	4.6	0.4	0.59	1.12
ROSACEAE	<i>Prunus</i>	200	15	4	5412	1080	7.5	2.0	3.59	8.93
	<i>Rosa</i>	150	12	5	1944	996	8.0	3.3	3.63	3.55
	<i>Rubus</i>	250	38	11	774	875	15.2	4.4	2.67	1.16
	<i>Spiraea</i>	100	13	3	97	77	13.0	3.0	0.31	0.20
FABACEAE	<i>Vicia</i>	140	13	1	1244	689	9.3	0.7	2.57	2.32
	<i>Lespedeza</i>	40	13	4	45	135	32.5	10.0	0.63	0.11
GERANIACEAE	<i>Geranium</i>	300	12	2	557	211	4.0	0.7	0.59	0.77
EUPHORBIACEAE	<i>Euphorbia</i>	2000	13	6	1250	953	0.7	0.3	0.75	0.46
SAPINDACEAE	<i>Acer</i>	111	26	23	1948	638	24.3	20.7	2.52	3.88
AQUIFOLIACEAE	<i>Ilex</i>	400	23	7	1221	290	5.8	1.8	0.71	1.45
CELASTRACEAE	<i>Euonymus</i>	177	18	5	85	63	10.2	2.8	0.22	0.15
ELAEAGNACEAE	<i>Elaeagnus</i>	40	15	11	58	39	37.5	27.5	0.18	0.14
VIOLACEAE	<i>Viola</i>	400	55	13	1136	723	13.8	3.3	1.76	1.35
ONAGRACEAE	<i>Epilobium</i>	165	12	0	348	196	7.3	0.0	0.69	0.62
APIACEAE	<i>Angelica</i>	110	23	16	281	135	20.9	14.5	0.54	0.56
ERICACEAE	<i>Rhododendron</i>	850	51	42	2132	866	6.0	4.9	1.32	1.56
	<i>Vaccinium</i>	450	19	7	614	572	4.2	1.6	1.31	0.68
SYMPLOCACEAE	<i>Symplocos</i>	250	23	11	693	110	9.2	4.4	0.34	1.04
PRIMULACEAE	<i>Lysimachia</i>	150	15	4	239	97	10.0	2.7	0.35	0.44
	<i>Primula</i>	425	14	10	2511	409	3.3	2.4	0.97	2.89
GENTIANACEAE	<i>Gentiana</i>	361	15	6	1005	397	4.2	1.7	1.02	1.26
APOCYNACEAE	<i>Cynanchum</i>	100	22	12	462	97	22.0	12.0	0.39	0.95
RUBIACEAE	<i>Galium</i>	300	18	4	87	169	6.0	1.3	0.48	0.12
VERBENACEAE	<i>Callicarpa</i>	140	10	5	124	65	7.1	3.6	0.24	0.23
CAPRIFOLIACEAE	<i>Lonicera</i>	180	21	11	656	145	11.7	6.1	0.50	1.13
	<i>Viburnum</i>	150	16	5	463	194	10.7	3.3	0.71	0.85

Table 1. (Continued)

Family	Genus	No. of species in the world	No. of native species in Japan	No. of endemic species in Japan	Nucleotide sequences on web	Literature titles on web	Relative species richness in Japan (%)	Relative endemic richness in Japan (%)	LCI ^a	NCI ^b
LAMIACEAE	<i>Ajuga</i>	50	13	8	30	76	26.0	16.0	0.35	0.07
VERONICACEAE	<i>Veronica</i>	180	13	5	945	213	7.2	2.8	0.73	1.62
OROBANCHACEAE	<i>Pedicularis</i>	350	15	8	568	157	4.3	2.3	0.41	0.73
LENTIBULARIACEAE	<i>Utricularia</i>	180	11	1	246	266	6.1	0.6	0.92	0.42
CAMPANULACEAE	<i>Adenophora</i>	40	11	5	75	25	27.5	12.5	0.12	0.18
ASTERACEAE	<i>Artemisia</i>	350	30	7	948	896	8.6	2.0	2.34	1.21
	<i>Aster</i>	250	21	13	212	323	8.4	5.2	0.98	0.32
	<i>Chrysanthemum</i>	40	14	10	958	210	35.0	25.0	0.98	2.29
	<i>Cirsium</i>	250	52	50	321	166	20.8	20.0	0.51	0.48
	<i>Parasenecio</i>	60	14	12	117	42	23.3	20.0	0.19	0.26
	<i>Saussurea</i>	300	25	17	645	93	8.3	5.7	0.26	0.89
	<i>Senecio</i>	1250	12	4	1513	591	1.0	0.3	0.68	0.82
	<i>Taraxacum</i>	60	11	9	889	344	18.3	15.0	1.53	2.01

The five genera with the highest relative species/endemic richness in Japan are shown in bold. ^aLiterature collection index. ^bNucleotide collection index.

species number of the genus. For example, for genus *Calanthe*, which has 150 spp. worldwide, the numbers of literature titles and nucleotide sequences deposited online are 23 and 35, so LCI and NCI can be calculated as $0.08=23/(0.5428 \times 150+192.6)$ and $0.06=35/(1.172 \times 150+371.4)$, respectively. LCI and NCI for each of the species-rich angiosperm genera of Japan are listed in Table 1. Note that LCI and NCI are not fixed values and will change through time so one should update them before using it as the criteria for finding the plant genera under-/over-represented in research ad hoc.

In facing serious loss of plant diversity in Japan, it would be an important practice to quantitatively recognize the plant genera that are especially species-rich in Japan. It is also noteworthy that, in the perspective of comparative studies, species-rich genera are especially useful to draw robust conclusions, as more species enable more comparisons. In this study, five genera, *Hosta* (Agavaceae), *Tricyrtis* (Ruscaceae), *Asarum* (Aristolochiaceae), *Hydrangea* (Hydrangeaceae), and *Mitella* (Saxifragaceae), were found to have their center of diversity in Japan. The five genera tend to be underrepresented in the literature (LCI: 0.15–0.79; Table 1), although the number of nucleotide sequences varies among them (NCI: 0.13–2.48; Table 1), probably because the researchers outside Japan would have difficulty in access to most of the species. Because large information on ecological traits, including pollination systems, seed dispersal, habitat preferences, etc. is only available in the wild, the accumulation of natural history information and intensive field researches for these genera would be urgently needed.

In this study, I used two measures, i.e., number of literature titles and nucleotide sequences and proposed LCI and NCI as the corresponding criteria for quantifying the research effort for the plant genera. I would suggest LCI is the more reliable criterion, as the number of literature titles will not abruptly increase with a small research effort. In contrast, the number of nucleotide sequences deposited online can quick-

ly increase with only a small research effort such as a single molecular phylogenetic study.

In conclusion, the present quantification of research effort for 84 species-rich angiosperm genera of Japan highlighted its nonuniformity despite the presence of general tendency that is proportional to generic size. I hope the present brief survey serves as a good starting point to recognize the pattern of how information on natural history of the flora of Japan is distributed, and to establish efficient research strategies thereafter.

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References

- Aoki, K., Suzuki, T., Wsu, T.-W. and Murakami N. 2004. Phylogeography of the component species of broad-leaved evergreen forests in Japan, based on chloroplast DNA variation. *Journal of Plant Research* 117: 77–94.
- Environment Agency of Japan 2000. *Threatened Wildlife of Japan: Red Data Book*, 2nd edn. Japan Wildlife Research Center, Tokyo.
- Fujii, N., Tomaru, N., Okuyama, K., Koike, T., Mikami, T. and Ueda, K. 2002. Chloroplast DNA phylogeography of *Fagus crenata* (Fagaceae) in Japan. *Plant Systematics and Evolution* 232: 21–33.
- Fujii, N. and Senni, K. 2006. Phylogeography of Japanese alpine plants: biogeographic importance of alpine region of central Honshu in Japan. *Taxon* 55: 43–52.
- Ikeda, H., Senni, K., Fujii, N. and Setoguchi, H. 2006. Refugia of *Potentilla matsumurae* (Rosaceae) located at high mountains in the Japanese archipelago. *Molecular Ecology* 15: 3731–3740.
- Ikeda, H. and Setoguchi, H. 2006. Phylogeography of *Arctericia nana* (Maxim.) Makino (Ericaceae) suggests another range expansion history of Japanese alpine plants. *Journal of Plant Research* 119: 489–495.
- Ikeda, H. and Setoguchi, H. 2007. Phylogeography and refugia of the Japanese endemic alpine plant *Phylodoce nipponica* Makino (Ericaceae). *Journal of Biogeography* 34: 169–176.
- Iwatsuki, K., Yamazaki, T., Boufford, D. E. and Ohba, H. 1993. *Flora of Japan*, Vol. IIIa, Kodansha, Tokyo, Japan.
- Iwatsuki, K., Yamazaki, T., Boufford, D. E. and Ohba, H. 1995. *Flora of Japan*, Vol. IIIb, Kodansha, Tokyo, Japan.
- Iwatsuki, K. 1995. Species diversity in East Asia in a global perspective. In: Box, E. E. O., Peet, R. K., Masuzawa, T., Yamada, I., Fujiwara, K. and Maycock, P. F. (eds.), pp. 57–67. *Vegetation Science in Forestry*, Kluwer Academic, Dordrecht.
- Iwatsuki, K., Boufford, D. E. and Ohba, H. 1999. *Flora of Japan*, Vol. IIc, Kodansha, Tokyo, Japan.
- Iwatsuki, K., Boufford, D. E. and Ohba, H. 2001. *Flora of Japan*, Vol. IIb, Kodansha, Tokyo, Japan.
- Iwatsuki, K., Boufford, D. E. and Ohba, H. 2006. *Flora of Japan*, Vol. IIa, Kodansha, Tokyo, Japan.
- Kato, M., Kakutani, T., Inoue, T. and Itino, T. 1990. Insect-flower relationship in the primary beech forest of Ashu, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. *Contribution from the Biological Laboratory, Kyoto University* 27: 377–463.
- Kato, M., Matsumoto, M. and Kato, T. 1993. Flowering phenology and anthophilous insect community in the cool-temperate subalpine forests and meadows at Mt. Kushigata in the central part of Japan. *Contribution from the Biological Laboratory, Kyoto University* 28: 119–172.
- Kato M. 2000. Anthophilous insect community and plant-pollinator interactions on Amami Islands in the Ryukyu Archipelago, Japan. *Contribution from the Biological Laboratory, Kyoto University* 29: 157–252.
- Kato, M., Takimura, A. and Kawakita, A. 2003. An obligate pollination mutualism and reciprocal diversification in the tree genus *Glochidion* (Euphorbiaceae). *Proceedings of the National Academy of Science, USA* 100: 5264–5267.
- Kato, M. and Okuyama, Y. 2004. Changes in the biodiversity of a deciduous forest ecosystem caused by an increase in the Sika deer population at Ashu, Japan. *Contribution from the Biological Laboratory, Kyoto University* 29: 437–448.
- Mabberley, D. J. 1997. *The Plant-book. A Portable Dictionary of the Vascular Plants*. 2nd edition. Cambridge University Press, Cambridge.
- Martins, E. P. and Hansen, T. F. 1997. Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* 149: 646–667.
- Nakazawa, M., Wakabayashi, M., Ono, M. and Murata, J. 1997. Molecular phylogenetic analysis of *Chrysosplenium* (Saxifragaceae) in Japan. *Journal of Plant Research* 110: 265–274.
- Noma, N. and Yumoto T. 1997. Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research* 12: 119–129.

- Okuyama, Y., Fujii, N., Wakabayashi, M., Kawakita, A., Ito, M., Watanabe, M., Murakami, N. and Kato, M. 2005. Nonuniform concerted evolution and chloroplast capture: heterogeneity of observed introgression patterns in three molecular data partition phylogenies of Asian *Mitella* (Saxifragaceae). *Molecular Biology and Evolution* 22: 285–296.
- Okuyama, Y., Pellmyr, O. and Kato, M. 2008. Parallel floral adaptations to pollination by fungus gnats within the genus *Mitella* (Saxifragaceae). *Molecular Phylogenetics and Evolution* 46: 560–575.
- Ota, M., Imaichi, R., Kato, M. 2001. Developmental morphology of the thalloid *Hydrobryum japonicum* (Podostemaceae). *American Journal of Botany* 88: 382–390.
- R Development Core Team 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Satake, Y., Ohwi, J., Kitamura, S., Watari, S. and Tominari, S. 1981. Wild Flora of Japan: Harbaceous Plants. Heibonsha, Tokyo.
- Satake, Y., Hara, H., Watari, S. and Tominari, T. 1989. Wild Flora of Japan: Woody Plants. Heibonsha, Tokyo.
- Savolainen, V. and Chase, M. W. 2003. A decade of progress in plant molecular phylogenetics. *Trends in Genetics* 19: 717–724.
- Takahashi, H. 1994. A comparative study of floral development in *Trillium apetalon* and *T. kamschaticum* (Liliaceae). *Journal of Plant Research* 107: 237–243.
- Tobe, H. 2008. Embryology of *Japonolirion* (Petrosaviaceae, Petrosaviales): a comparison with other monocots. *Journal of Plant Research* 121: 407–416.
- Yamaji, H., Fukuda, T., Yokoyama, J., Pak, J.-H., Zhoue, C.-Z., Yang, C.-S., Kondo, K., Morota, T., Takeda, S., Sasaki, H. and Maki, M. 2007. Reticulate evolution and phylogeography in *Asarum* sect. *Asiasarum* (Aristolochiaceae) documented in internal transcribed spacer sequences (ITS) of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution* 44: 863–884.