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Title	Twenty years of community dynamics in a mixed conifer : broadleaved forest under a selection system in northern Japan
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1 **Twenty years of community dynamics in a mixed conifer-broadleaved**

2 **forest under a selection system in northern Japan**

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21 21 pages for the text, 3 tables, 7 figures

1   **Abstract:** Single tree selection has been employed widely in northern Japanese mixed forests, but

2   management-induced changes in forests are not been well understood. This study examined

3   demographic parameters of major tree species during 20-years in a 68-ha study stand, in which

4   single tree selection has been conducted since 1971. Results showed that conifers (mostly *Abies*

5   *sachalinensis*) gained the strongest positive effects from the treatment on growth and survival.

6   Nevertheless, recruitment of conifers was not sufficiently improved, suggesting their decreased

7   dominance over a longer-term. Instead, shade-intolerant broadleaved (mainly *Betula ermanii*) will

8   gradually increase because of their higher recruitment rates after the treatment. Shade-tolerant

9   broadleaved (mainly *Acer mono* and *Tilia japonica*) appeared to experience the most distinct

10   negative effects, especially on survival. These trends differed markedly from those reported in

11   previous papers concerning partial harvesting system, which predicted increase of shade-tolerant

12   species. The results shown here should be generalized carefully because we have investigated only

13   one stand without repetition of the control area. Nevertheless, trends described in this large-scale and

14   long-term study could provide a basis for simulating stand dynamics. We discussed possible reasons

15   for the observed patterns, and provided implications for sustainable management in the region.

16

1 Introduction

2   Recently, partial harvesting system is raising concerns about managing forests both for timber

3   production and ecosystem functions (Oliver and Larson 1996, Kohm and Franklin 1997, von Gadow

4   et al. 2002) because it often engenders stands with complex structure and composition (O'Hara 1998,

5   Deal 2001, Deal and Tappeiner 2002, Harvey et al. 2002). In a northern Japanese mixed

6   conifer-broadleaved forest (including *Abies*, *Picea*, *Acer*, *Tilia*, *Quercus*, *Betula*, etc.), a typical

7   forest type of that region (Tatewaki 1958), a selection system (single tree selection) has been widely

8   employed since its exploitation period (early 20th century) as a superior option to manage natural

9   forests. Most forests have experienced at least one instance of harvesting in the past. However,

10   despite silviculture basic principles (e.g. Smith et al. 1997), actual harvesting practices were often

11   excessive and showed preferential extraction of large trees (Nagaike et al. 1999), thereby degrading

12   regional forests. Most previous studies of harvesting practices in northern Japan have emphasized

13   sustainable yields (Ohgane et al. 1988, Nigi et al. 1998); few studies have examined broader

14   objectives, including maintenance of biodiversity. Contributing factors for ecosystem integrity

15   (Hunter 1999) such as changes in stand structure and tree species composition have not been well

16   understood.

17   Sustainable forestry may attempt to mimic natural disturbances through management practices

18   (Spence 2001, Franklin et al. 2002, Mitchell et al. 2002). The natural disturbance regime of northern

19   Japanese mixed forests is a combination of rare large-scale blowdown ($> 10^4$ m^2: note that fire is

20   unimportant in this region) and frequent small-scale tree death ($< 10^3$ m^2: Ishikawa and Ito 1984,

21   Kubota 1995, Nakashizuka and Iida 1995). Although little information is available regarding the

22   large-scale disturbances in this region, several previous studies have predicted that the establishment

23   of some major component tree species, including *Betula ermanii* Cham., *Quercus crispula* Bl. and

24   *Abies sachalinensis* (Fr. Schm.) Masters, is related closely to large-scale disturbances (Suzuki et al.

25   1987, Sano 1988, Ishikawa and Ito 1989, Osawa 1992, Ishizuka et al. 1998). On the other hand, as

1   shown in many other regions (Hibbs 1982, Runkle 1985, Tanaka and Nakashizuka 1998),

2   small-scale disturbances have been shown to have a fundamental influence on the structure of these

3   natural forests. Natural tree mortalities in terms of basal area observed in this region were frequently

4   less than 1% year^{-1} (Hiura and Fujiwara 1999, Kubota 2000); some major tree species (*Abies*

5   *sachalinensis*, *Acer mono* Maxim. and *Sorbus commixta* Hedl.) regenerate in the resultant canopy

6   gaps (Ishizuka 1984, Kubota et al. 1994, Hiura et al. 1996, Kubota 2000, Takahashi et al. 2003).

7   This study was intended to present implications for sustainable harvesting system, particularly

8   through evaluating the effects on tree species composition. Single tree selection superficially

9   resembles a small-scale disturbance regime (creation of canopy gaps), but it engenders some

10   fundamental differences, such as removal of stems and the consequent reduction of fallen trees

11   (Noguchi and Yoshida 2004). In a mixed forest, we can therefore predict that single tree selection

12   generally enhances the establishment and growth of particular species that adapt ecologically to

13   small canopy gaps (cf. Runkle 1982, Runkle and Yetter 1987, Canham and Marks 1985, Abe et al.

14   1995, Messier et al. 1999). Actually, some North American studies have reported that dominance of

15   shade-tolerant species gradually increases after single tree selection (Leak and Fillip 1977, Jenkins

16   and Parker 1999, Webster and Lorimer 2002, Shuler 2004). Nevertheless, such a trend in

17   compositional change may differ among forest types. Constituent species probably adapt to inherent

18   environmental conditions and interspecific relationships, both of which can be strongly affected by

19   harvesting treatment. The northern Japanese mixed forest is characterized by a relatively large gap

20   area in the canopy layer, which is often more than 20% (Ishikawa and Ito 1985, Kubota 1995, 2000,

21   Takahashi et al. 2003). This characteristic is conspicuously apparent in heavy snowfall regions; it is

22   inferred to be related to slow recruitment rate caused by dense undercover of dwarf bamboo species

23   (*Sasa kurilensis* (Rupr.) Makino et Shibata or *S. senanensis* (Franch. et Savat.) Rehd.) (Takahashi

24   1997, Umeki and Kikuzawa 1999). Small trees may not respond directly to single tree selection

25   because dwarf bamboos increasingly dominate the canopy gaps (Noguchi and Yoshida 2005, cf.

1   Messier et al. 1998).

2   The specific questions we address by this study are: (1) Does a single tree selection change tree

3   species composition? and (2) If change occurs, does it correspond to the expectations derived from

4   characteristics (e.g. shade-tolerance) of constituent species? We examined 20 years of community

5   dynamics of a mixed conifer-broadleaved forest in northern Japan under a selection system by which

6   single tree selection at ten-year intervals had been conducted since 1971. We compared demographic

7   parameters of major component tree species (and species groups) between treated and untreated

8   areas based on a repeated census of ca. 27,000 individuals in a large (68-ha) plot. We summarized

9   species recovery for that period and discussed long-term effects of single tree selection on stand

10   structure and species composition in the region.

11

12   **Methods**

13   This study was conducted in the Nakagawa Experimental Forest of Hokkaido University (44° 48'

14   N, 142º 14' E, 150 m in elevation; Fig. 1). The forest is located in a cool-temperate region with

15   heavy snowfall in winter. Typical vegetation in the Nakagawa forest is mixed conifer-broadleaved

16   forest, as described by Tatewaki and Igarashi (1971). This type of forests are widely distributed in

17   north-eastern Asia as a representative natural vegetation (Tatewaki 1958), and are responsible for

18   regional biodiversity. The mean annual temperature is 5.4°C and the mean precipitation is 1,449 mm.

19   Nearly half of the precipitation falls in the non-growing season (November–April). Snow cover

20   usually extends from early November to early May, with a maximum depth of 200 cm. The soils are

21   classified as Inceptisol (acidic brown forest soil), and the predominant bedrock is Cretaceous

22   sedimentary rock (Tatewaki and Igarashi 1971).

23   Since 1967, a long-term study has been conducted at a 110-ha study site (Fig. 1, Table 1). Few

24   large-scale disturbances or outbreaks were recorded during the study period, which enabled us to

25   evaluate effects of selection harvesting clearly. The primary objective of the original study was to

1 develop a relevant management system to extract sustainable yield (Ohgane et al. 1988, Nigi et al.

2 1998). The 'check method' presented by Knuchel (1953), which intend to maintain timber volume

3 and quality in the stand, have been applied (see below for detailed practices).

4   The original stand had a multiaged structure that was similar to those of other mixed forests in the

5 region (Suzuki et al. 1987, Takahashi et al. 2003). Before the plot establishment, the stand had been

6 partially harvested for domestic fuel materials with very low intensity. The sum of the basal area at

7 the first census (i.e. pre-harvest basal area) was 29.9 m^2 ha^{-1}, which was typical of the region. There

8 appeared 27 tall-tree species in all (4 evergreen conifers and 23 deciduous broadleaved species), of

9 which *Abies sachalinensis* shared nearly half of the total basal area, with lesser areas occupied, in

10 descending order, by *Acer mono*, *Tilia japonica* (Miq.) Simonkai, *Quercus crispula*, *Betula ermanii*,

11 and others. (see Table 2).

12   The forest was divided into 11 compartments (areas ranging 5.6–17.6-ha) including a control

13 compartment (5.9-ha). The dominant species showed no strong preferences in their spatial

14 distributions (T. Yoshida, unpublished), and tree species compositions before the treatments were

15 similar among the compartments. A selection system was employed, by which single tree selections

16 were conducted at 10-year intervals (one compartment per year). This study analyzed 20 years of

17 data (i.e. two rounds of harvesting) from six compartments and the control (68-ha in all) within

18 which 27,300 trees were censused individually and identified with numbered tags. The compartment

19 No.1-4 were not subjected in this study, because their census were conducted without individual

20 identifications. The area, the sum of the basal area, and harvested level of the compartments are

21 shown in Table 1. The mean harvested level in terms of basal area was 19% (range 10–28%) for the

22 first treatment and 16% (range 12–18%) for the second. These intensities were determined carefully

23 in consideration of the census data, to maintain harvested volume equivalent to the growth (i.e.

24 volume increment) of the compartments. In these harvestings, trees with a lower timber value (i.e.

25 with injury, crack, etc.) were selected mainly to improve the future economic quality of the stand.

1   Nevertheless, the harvested trees were selected from a broad range of size classes, and showed no

2   bias to any particular tree species; the total amounts of harvested conifers and harvested broadleaved

3   were roughly equal.

4   Harvestings were conducted in winter. Trees were felled and their major branches were cut

5   immediately by hand using a chain saw. Then the logs were extracted using a tractor (a sled was used

6   only in a few early years). Snow, normally 100–200 cm deep, covered the forest floor. Consequently,

7   soil disturbances that typically accompany treatments were minor. Although supplemental plantings

8   were conducted for some large non-wooded openings (e.g. canopy gaps larger than 400 m^2), we did

9   not consider them in this study because they are still young and planted trees did not reach the lower

10   limit size set for the census (see below). More detailed descriptions of the practices are available in

11   Ohgane et al. (1988).

12   In the 68-ha area, 27,300 trees were identified with diameter at breast height (DBH) $\geq$ 12.5 cm.

13   The DBH-classes (5 cm interval) of all living trees were determined by measurement in the year

14   before treatment. Checks of survival or death, repeated measures of the DBH-class, and records of

15   newly recruited trees were carried out in the second and third census. The basal area of individuals

16   was calculated using the median of the DBH-class. We calculated the following demographic

17   parameters.

18   [1]   Tree DBH-class promotion rate $= [(N + N_p)/N]^{0.1} - 1$

19   [2]   Tree mortality $= 1 - [(N - N_d)/N]^{0.1}$

20   [3]   Tree recruitment rate $= [(N + N_r)/N]^{0.1} - 1$

21   where N represents the initial tree number (except for harvested trees); N_p is the number of trees that

22   promote their DBH-class to the next; N_d is the number of naturally dead trees; and N_r is the number

23   of recruited trees during the ten-year period. Compartments with exceptional intervals (eight or nine

24   years) in the first period were calculated separately; then the weighted averages by area were used as

25   a representative value. We calculated these indices for four size classes (DBH: 12.5– 22.4, 22.5–

1   32.4, 32.5–42.4, and over 42.4 cm [in case of the DBH-promotion rate, 42.5–52.4 cm]) by species.

2   In addition, species were grouped into 'conifer', 'shade-tolerant broadleaved', and 'shade-intolerant

3   broadleaved' to summarize the results. The 'conifer' group consists of four shade-tolerant species,

4   represented mostly by *Abies sachalinensis*. The broadleaved species were classified with reference

5   to previous studies of physiological traits (Koike, 1988) or regeneration mode in an old-growth stand

6   (i.e. species with abundant smaller trees are assumed to be shade-tolerant: Masaki 2002) (Table 2).

7   Conifers shared nearly half of the total basal area: shade-tolerant (dominated by *Acer mono* and *Tilia*

8   *japonica*) and shade-intolerant broadleaved species (dominated by *Quercus crispula* and *Betula*

9   *ermanii*) respectively shared a quarter.

10

11 Results

12 **Growth**

13 The DBH-class promotion rates of the treated area were lower than those in the control (about 0.8

14 times) in the first period, but turned higher (about 1.5 times) in the second period in all the

15 DBH-classes (Fig. 2). Improvement in the second period was particularly apparent for conifers, but

16 not so distinct for broadleaved. A markedly high promotion rate was shown in the largest DBH-class

17 (42.5–52.4 cm) of shade-intolerant broadleaved in the control, but it was not followed by that in the

18 treated area, even in the second period.   In the first period, nearly half of the species had lower

19 DBH-promotion rates in the treated area than that in the control (Fig. 3). In the smallest DBH-class

20 (12.5–22.4 cm), shade-tolerant broadleaved tended to show higher rates, whereas shade-intolerant

21 broadleaved tended to show lower rates. Nevertheless, in the larger DBH-classes (≥32.5 cm), a

22 shade-intolerant broadleaved species, *Quercus crispula*, which generally showed the highest

23 promotion rate among species in the control, showed a considerably lower rate. In the second period,

24 although the apparent decrease in the treated area remained only in *Quercus crispula* in the largest

25 DBH-class (42.5–52.4 cm), most of species improved the rate. A shade-tolerant conifer, *Abies*

1   *sachalinensis*, showed the highest promotion rates among species in the treated area in all the

2   DBH-classes in the second period.

3   **Natural mortality**

4   Natural mortality in the second period of the larger DBH-classes ($\geq$32.5 cm) in the treated area

5   was considerably lower than that in the control when considering all species (Fig. 4). This trend

6   largely reflected that of conifers, and the respective mortalities of broadleaved (both shade-tolerant

7   and shade-intolerant) in the treated area were rather higher than those in the control. Among

8   shade-tolerant broadleaved, the increase in mortality in the smallest DBH-class (12.5–22.4 cm) was

9   remarkable.

10   The species' trends (Fig. 5) demonstrated that the range of natural mortality among species was

11   generally smaller in the treated area than in the control: species with higher mortality in the control

12   tended to show a lower mortality rate, and vice versa. Trees in the larger DBH-classes ($\geq$32.5 cm)

13   exhibited generally lower mortality in the second period. In contrast, for trees in the smaller

14   DBH-classes (<32.5 cm), the change between the periods was small; it showed no general trend

15   among species.

16   **Recruitment**

17   For the three species groups, recruitment rates in the treated area in the first period were similar to

18   that in the control, and doubled in the second period (Fig. 6). The recruitment rate of

19   shade-intolerant broadleaved was highest: in the second period, it was roughly two and three times

20   higher than those of shade-tolerant broadleaved and conifers, respectively. Although shade-tolerant

21   broadleaved had the lowest recruitment rate among the groups in the control, they showed greatest

22   improvement. In contrast, the improvement was smallest for conifers.

23   Five species (four shade-intolerant broadleaved and one conifer) had lower recruitment rates in the

24   treated area (Fig. 7). However, in the second period, almost all the subjected species were over the

25   equivalence line (i.e. the treated area showed higher rates than the control), with considerable

1 improvement of shade-intolerant broadleaved (such as *Betula ermanii* and *Salix* sp.). In contrast to

2 the control, *Abies sachalinensis* showed the lowest rate among all species in the treated area.

3 Shade-tolerant broadleaved did not show a clear trend among species.

4 **Change in basal area**

5 Table 3 summarizes changes in basal area of species (and species groups) during the 20 year

6 period. In total, 87% of the harvested basal area was recovered in the period; conifers showed

7 considerably higher recovery (112%). Three minor conifers (*Picea jezoensis* (Sieb. et Zucc.) Carr.),

8 *Picea glehnii* (Fr. Schm.) Masters, and *Taxus cuspidate* Sieb. et Zucc.) showed a similar trend to that

9 of *Abies sachalinensis*. These high recoveries were contributed mainly by high growth, and less so

10 by recruitment.

11 In contrast, the recovery of shade-tolerant broadleaved remained only 48%, reflecting both low

12 growth and high mortality. In particular, species with high dead basal area (*Acer mono*, *Sorbus*

13 *alnifolia* (Sieb. et Zucc.) C. Koch and *Prunus sargentii* Rehd.), exhibited the lowest recovery.

14 Shade-intolerant broadleaved showed intermediate recovery (85%), with high contribution of

15 recruitment. The species with lowest recoveries (*Magnolia obovata* Thunb., *Alnus hirsuta* Turcz. and

16 *Betula maximowicziana* Regel) in this group also showed high dead basal area.

17

18 **Discussion**

19 Demographic parameters of tree species and species groups differ widely between the treated area

20 and the control; the response to the single tree selection changed considerably between the first and

21 second periods. Such a temporal change in the response may be attributable to delay in the response

22 of trees (e.g. Oliver and Larson 1996, Youngblood and Ferguson 2003) and a cumulative effect of

23 repetitive harvestings. General expectations of selection harvesting are increased growth, recruitment,

24 and survival of trees, all positive effects, to compensate the loss of harvested trees. Actually, opposite

25 and negative effects were dominant in the first period.

1   Many previous studies have suggested that partial harvesting system can maintain structural

2   complexities of the stand (Deal 2001, Deal and Tappeiner 2002). We can expect that the multiaged

3   structure of this stand was generally maintained because harvested trees were selected from a broad

4   range of size-classes. Nevertheless, our results showed clearly that the selection harvesting changes

5   tree species composition, even if basal area levels are nearly maintained. Although longer-term

6   trends do not necessarily follow the observed characteristics of demography, we could applied those

7   results for predicting stand dynamics. In the short term (i.e. several decades), *Abies sachalinensis*

8   will increase dominance relative to broadleaved because it gained the strongest positive effects from

9   selection harvesting on growth and survival. Such a positive response to small scale canopy

10   disturbances has already been reported in natural forests (Hiura et al. 1996, cf. Veblen 1986),

11   probably because of the physiological ability of *Abies* spp. to rapidly respond to increased light

12   availability (Noguchi et al. 2003, cf. Kneeshaw et al. 1998, Youngblood and Ferguson 2003).

13   Nevertheless, we found that recruitment of this species was not sufficiently improved after the

14   treatment: it was the lowest among major tree species. This trend should engender a lack of

15   small-sized trees and decreased dominance of this species over the long-term (i.e. more than one

16   hundred years).

17   Past studies have shown two different regeneration modes of *Abies sachalinensis*: continuous age

18   distribution suggesting dependence for its regeneration on small-scale disturbances (Ishizuka 1984,

19   Takahashi et al. 2003) and discontinuous distribution suggesting importance of large-scale

20   disturbances (Suzuki et al. 1987, Ishikawa and Ito 1989). The present results are, at least, not

21   consistent with the former. We presume that the limited recruitment is explained by 1) contrary to

22   growth improvement (see above), photosynthesis of *Abies sachalinensis* was found to decrease in

23   response to severe increased light availability especially in the dry summer (Noguchi et al. 2003, cf.

24   Kneeshaw et al. 2002, Bourgeois 2004), 2) because seedlings and saplings of this species are

25   frequently distributed around the stems of overstory trees (Suzuki et al. 1987, Takahashi 1997), they

1   may be affected greatly by physical damage accompanying the treatments (Harvey and Bergeron

2   1989). In general, it has been predicted that conifers are more vulnerable to such physical damage

3   than broadleaved species because of general inability to sprout (Greene et al. 1999). Furthermore,

4   because conifers base their establishment largely on fallen logs as a preferable substrate (Hiura et al.

5   1996), the possible decrease in fallen logs resulting from repetitive selection harvestings (Noguchi

6   and Yoshida 2004) may accelerate that decreasing trend over a longer-term. This tendency should be

7   more apparent in minor conifer species in this forest (but common in the region), *Picea jezoensis* and

8   *P. glehnii*, which show a particular dependency upon fallen logs (Kubota et al. 1994, Takahashi

9   1997).

10   Despite increased light availability after the selection harvesting, growth improvement of

11   shade-intolerant broadleaved species was less than that of *Abies sachalinensis*. Even in the second

12   period, large-sized trees in the treated area had considerably lower growth than those in the control;

13   their mortality did not decrease after the treatment. These facts seem to greatly reflect the trend of

14   *Quercus crispula*, but its small-sized trees showed an improved response (also see Yoshida and

15   Kamitani 1998). A great difference might exist in response to canopy opening between size classes.

16   *Quercus crispula* had discontinuous age distribution in natural mixed stands (Sano 1988; Takahashi

17   et al. 2003), suggesting the lower contribution of small-scale disturbances. Our results are consistent

18   with this hypothesis. Regarding other shade-intolerant broadleaved species, we found improved

19   growth in small sized *Betula ermanii* and *Alnus firma*, and decreased mortality in mid-sized

20   *Magnolia obovata* and *Kalopanax pictus* (Thunb.) Nakai. These are expected results in consideration

21   of responses to high light availability (Ishikawa and Ito 1989). These species also showed higher

22   recruitment rates after the treatment, which may contribute considerably to their recovery. They may

23   gain a relative advantage because their potential high growth rate occasionally enables them to

24   escape faster from the understory to a lighter environment. We can expect these species to gradually

25   increase in density after several decades.

1   In contrast, shade-tolerant broadleaved species appeared to incur the most distinct negative effects

2   from the treatment. Recovery of the basal area (percentage of the increment to that lost) in the

3   20-year period was only 48%; in particular, those of *Acer mono*, *Sorbus alnifolia* and *Prunus*

4   *sargentii* were less than 40%. These low recoveries were contributed mainly by high mortality,

5   presumably resulting from increased risks of wind or frost damage through canopy exposure (Peltola

6   et al. 1999). In addition, we found no distinct positive effects of the treatment on growth of these

7   species. Despite some exceptions (e.g. small-sized *Ulmus davidiana* Planch. var. japonica (Rehd.)

8   Nakai and *Sorbus alnifolia*), growths of dominant species (*Acer mono* and *Tilia japonica*) were

9   unchanged or decreased in the treated area. This trend is consistent with a previous finding that these

10   species showed low plasticity of growth against high light availability (Umeki 2001). In contrast,

11   recruitment of this species group increased in the second period, showing the greatest improvement,

12   compared with the control, among the three species groups. However, the absolute amount of

13   recruitment was still half that of shade-intolerant species.

14   Our study demonstrated complicated responses of the mixed species community under the

15   selection system. The observed trends of change in species composition differ markedly from those

16   reported in North America (Leak and Fillip 1977, Jenkins and Parker 1999, Webster and Lorimer

17   2002, Shuler 2004). We suspect that this difference is attributable to large canopy gap areas in the

18   overstory and dominance of dwarf bamboo species in this forest's understory. Selection harvesting,

19   and its consequent creation of canopy gaps, increases dwarf bamboos (Noguchi and Yoshida 2005),

20   which thereby suppresses tree regeneration (Hiura et al. 1995, Nagaike 1999, Umeki and Kikuzawa

21   1999). Those two distinct characteristics are closely correlated. We presume that the results are

22   informative, even for management of stands with rich understory vegetation (e.g. Harvey and

23   Bergeron 1989, Messier et al. 1998, Beckage et al. 2000, Bourgeois 2004), where such an indirect

24   negative effect of harvesting on light availability seems to occur.

25   The present results should be generalized carefully because we have investigated only one 68-ha

stand without repetition of the control area. Nevertheless, trends described in this large-scale and long-term study present implications for improving current harvesting practices. Attention should be devoted to the possible change in species composition toward shade-intolerant broadleaved, which might alter the ecosystem integrity of these mixed forests. Management plans must mitigate the negative effects of selection harvesting on growth, survival, and recruitment of particular species. For conifer species, supplemental planting or site preparation for natural regeneration (Wurtz and Zasada 2001, Yoshida et al. 2005) should be included to enhance their recruitment. At the same time, with considering the distinct negative effects, harvesting level of shade-tolerant broadleaved species should be limited to preserve their relative dominance. We need more detailed mechanisms by which observed patterns and processes are produced. In particular, we note that the amount of recruitment in this study might depend largely on pre-harvesting accumulation of a seedling bank because most of the recruited trees seemed to be older than 20 years (H. Miya, unpublished). Longer-term studies or those examining dynamics of seedlings and saplings (Noguchi and Yoshida, in preparation) are needed. In addition, we should consider site variations in the stand. Further studies that include responses of individual trees with spatial consideration (Noguchi and Yoshida, in preparation) are expected to yield additional important information. Together with the results of the current study, these extension studies can form an appropriate basis for adaptive management in this region.

1

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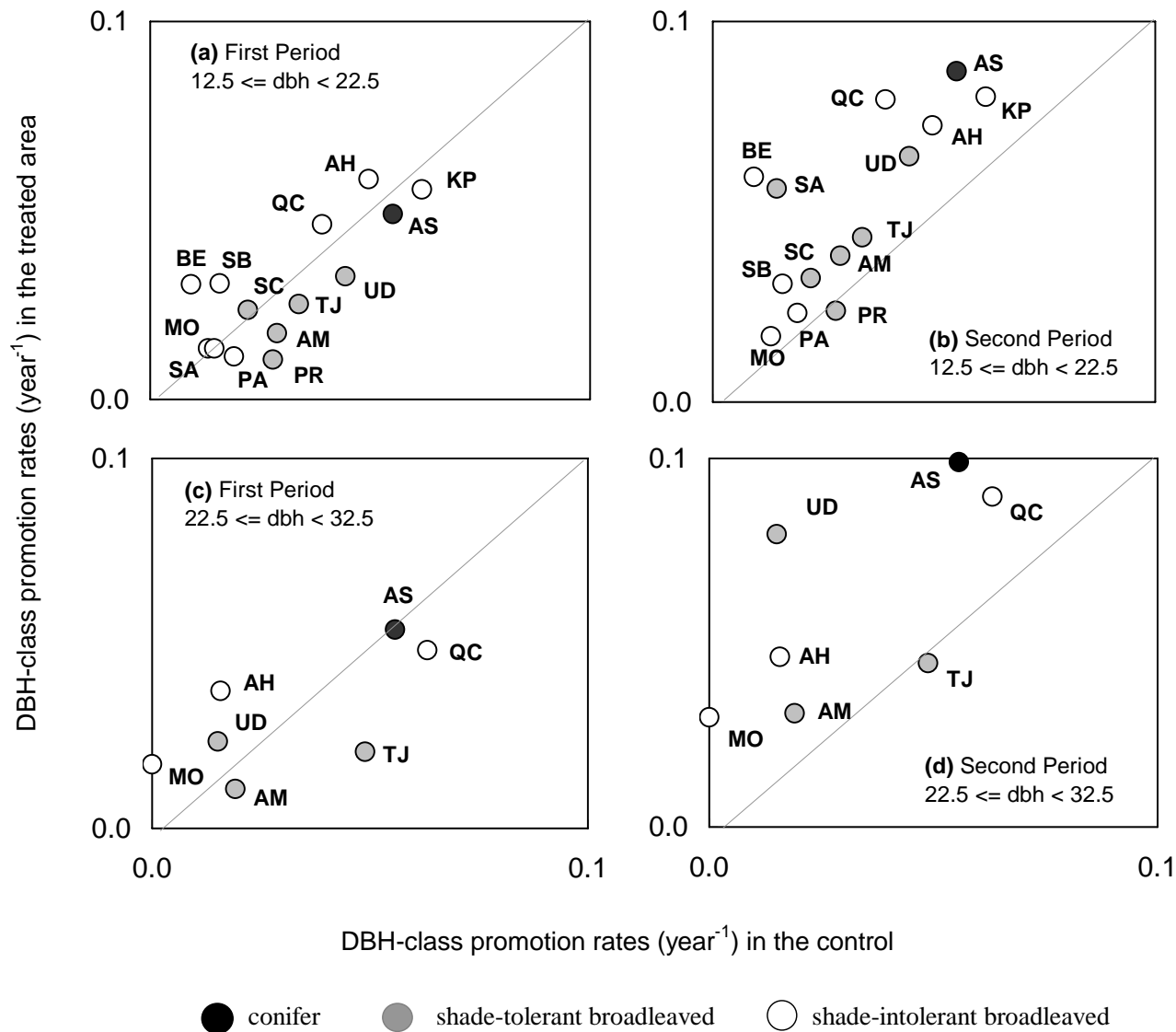6   seedlings after partial overstory canopy removal. Can. J. For. Res. **33**: 1315-1322.
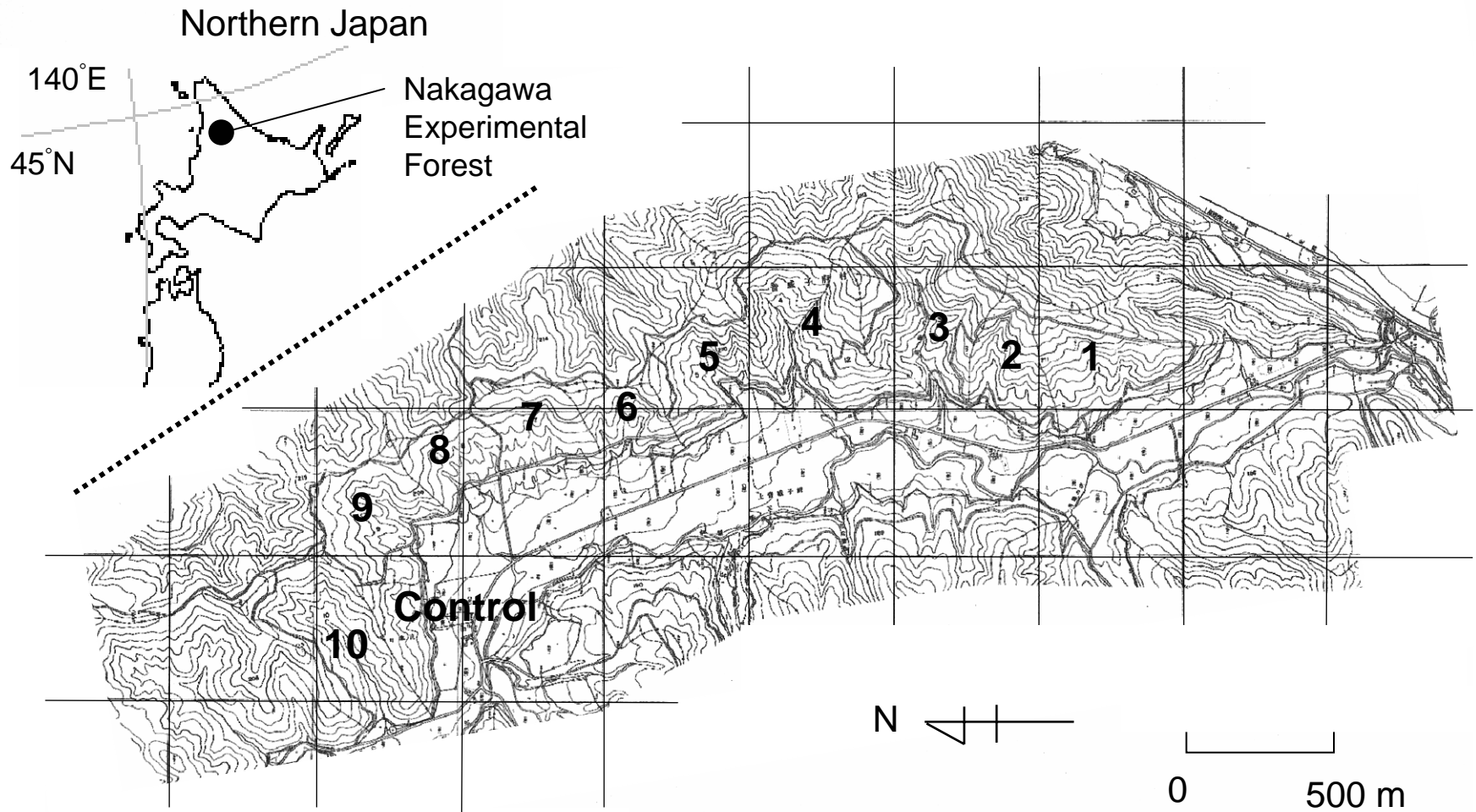
Fig. 1. Location and topography of the study area. Compartments 5-10 (62.1 ha) and the control (5.9 ha) were studied.
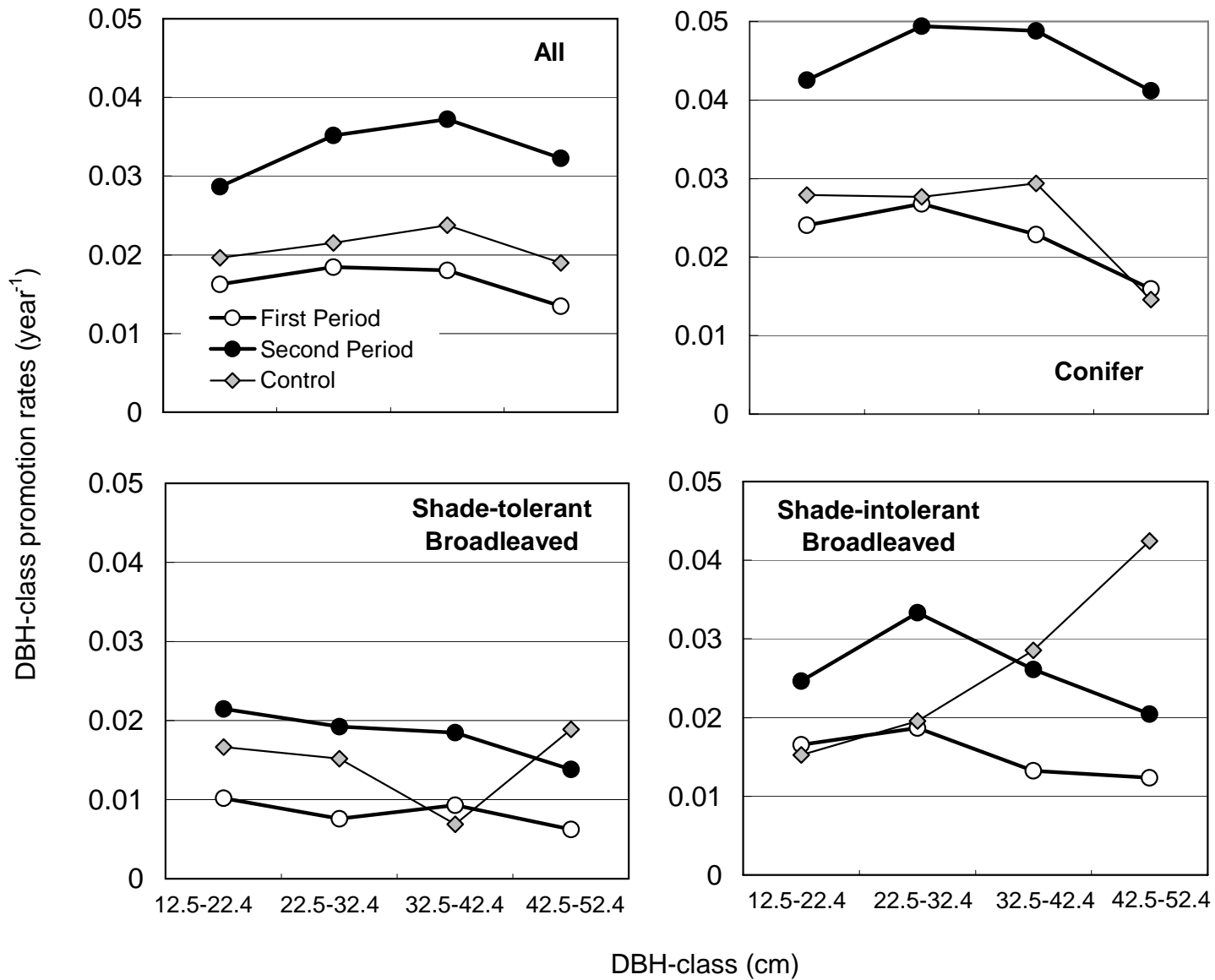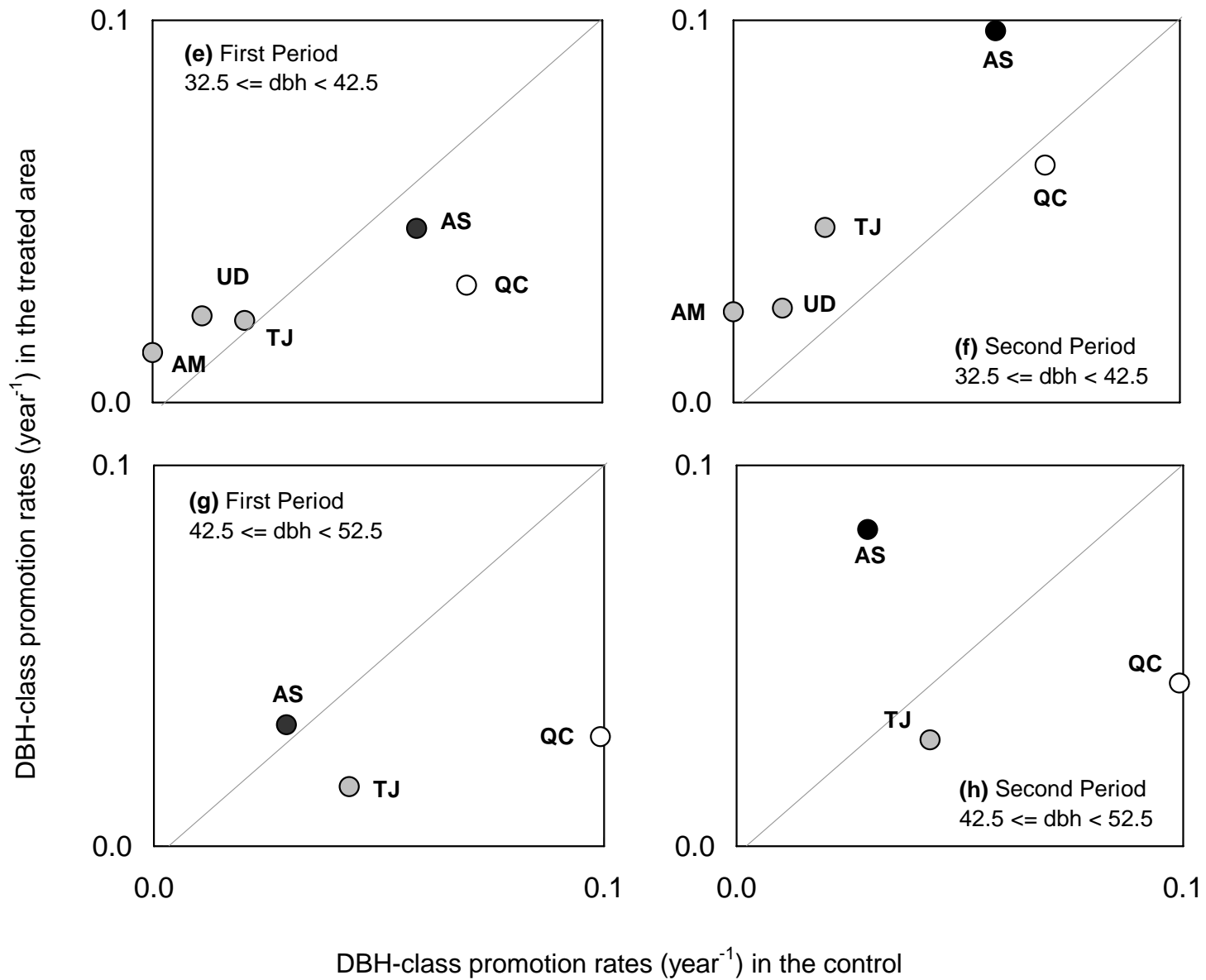
Fig. 2. The DBH-class promotion rates (year^{-1}) in the treated area (first and second period) and the control.
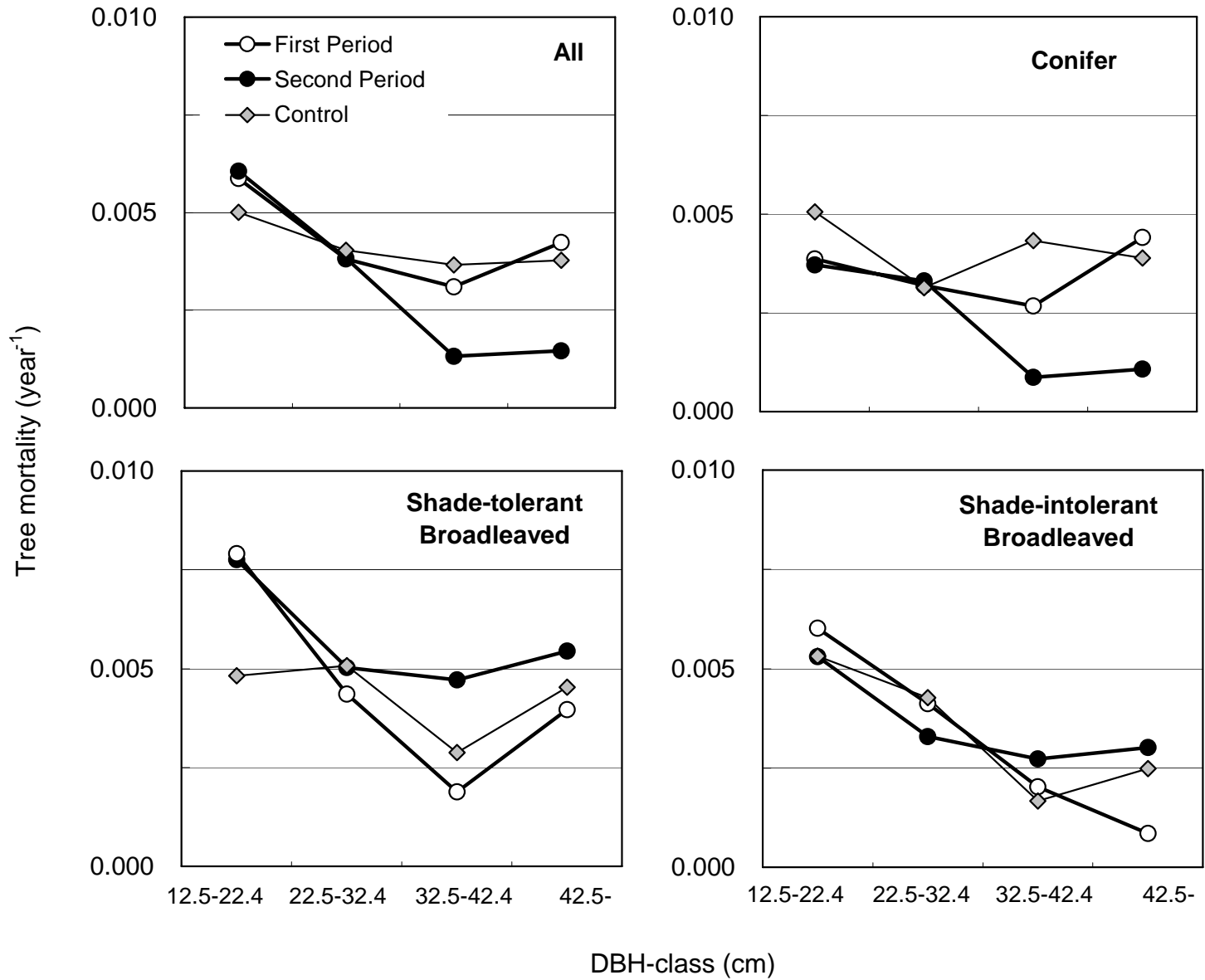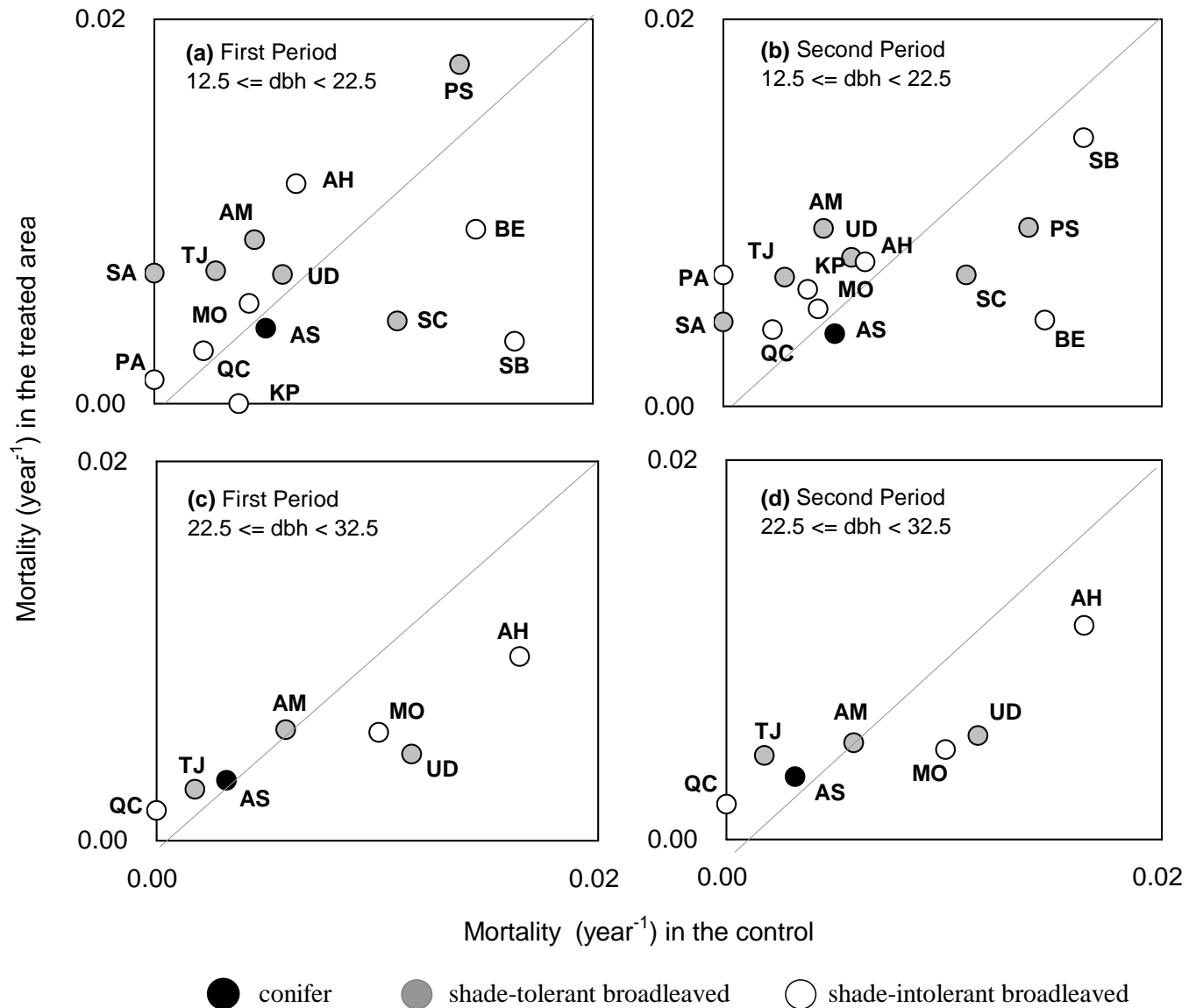
Fig. 3. Scatterplots of the DBH-class promotion rates (year^{-1}) for major tree species in the treated area (first and second period) against those in the control. Spicies abbreviations are shown in Table 2.

Fig. 3. *Continued*

Fig. 4. Tree mortality (year^{-1}) in the treated area (first and second period) and the control .

Fig. 5. Scatterplots of tree mortalities (year^{-1}) for major tree species in the treated area (first and second period) against those in the control . Spicies abbreviations are shown in Table 2.

Fig. 5. *Continued*

Fig. 6. Tree recruitment rate (year^{-1}) in the treated area (first and second period) and the control.

Fig. 7. Scatterplots of tree recruitment rates (year^{-1}) for major tree species in the treated area (first and second period) against those in the control. Spicies abbreviations are shown in Table 2.
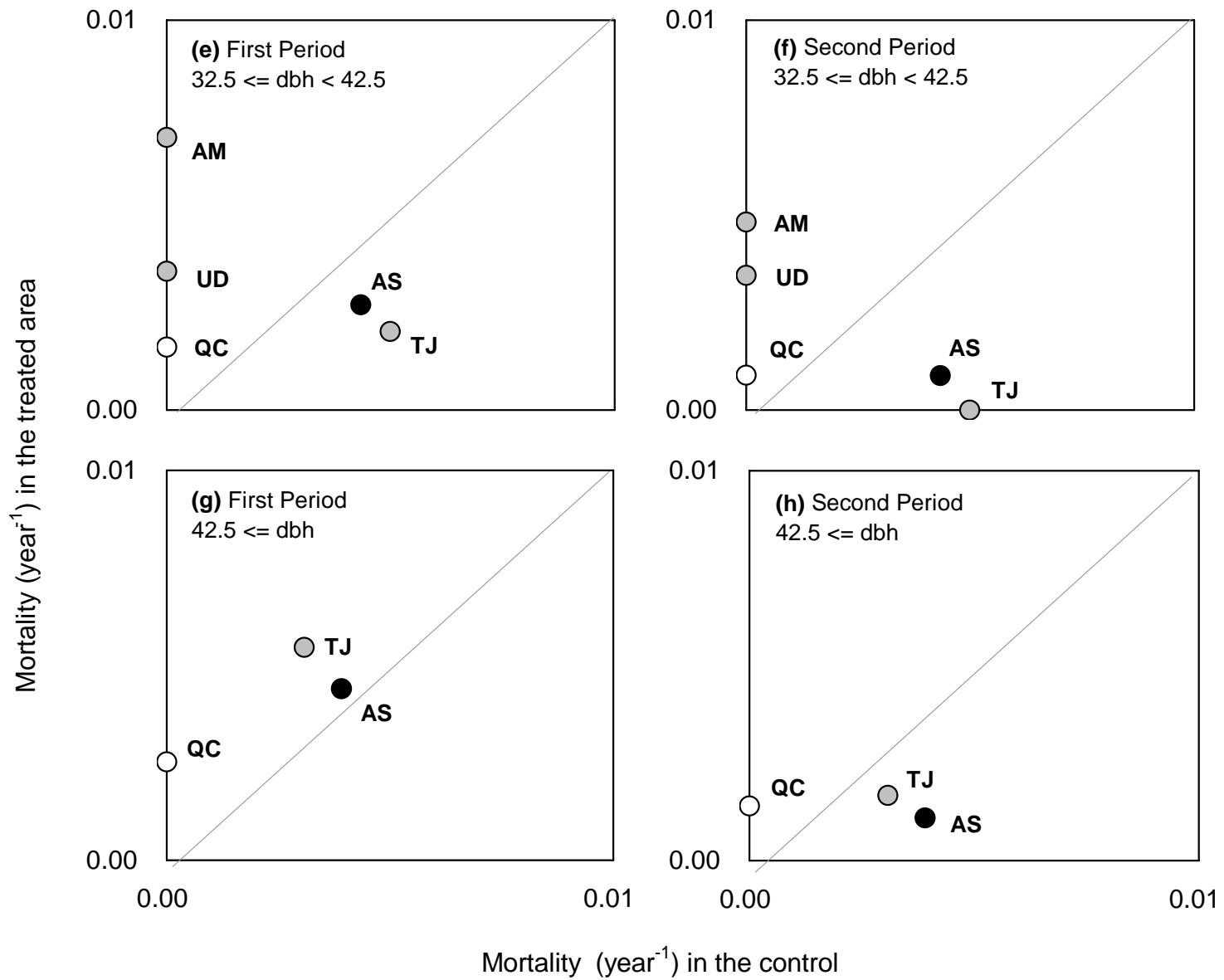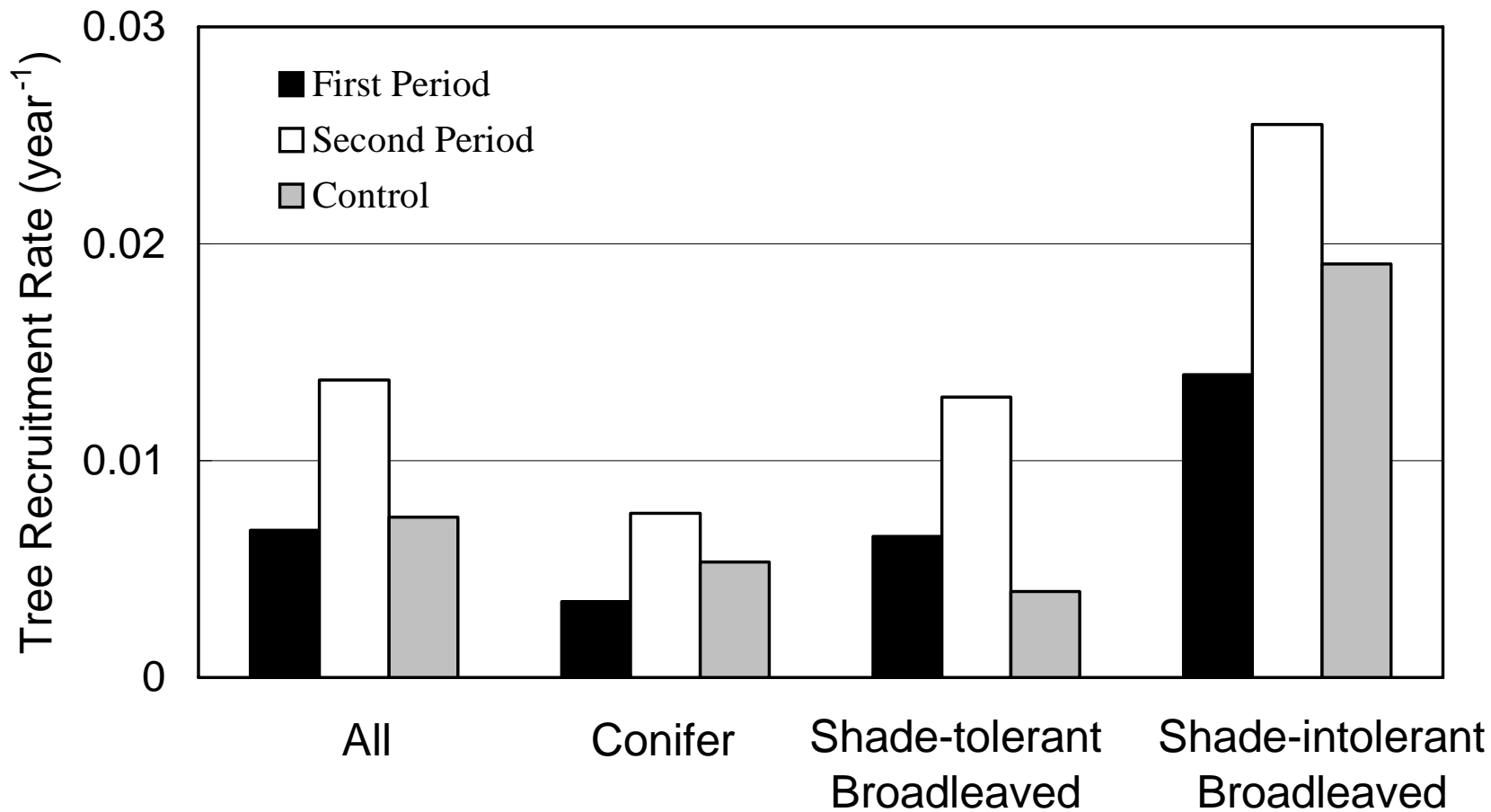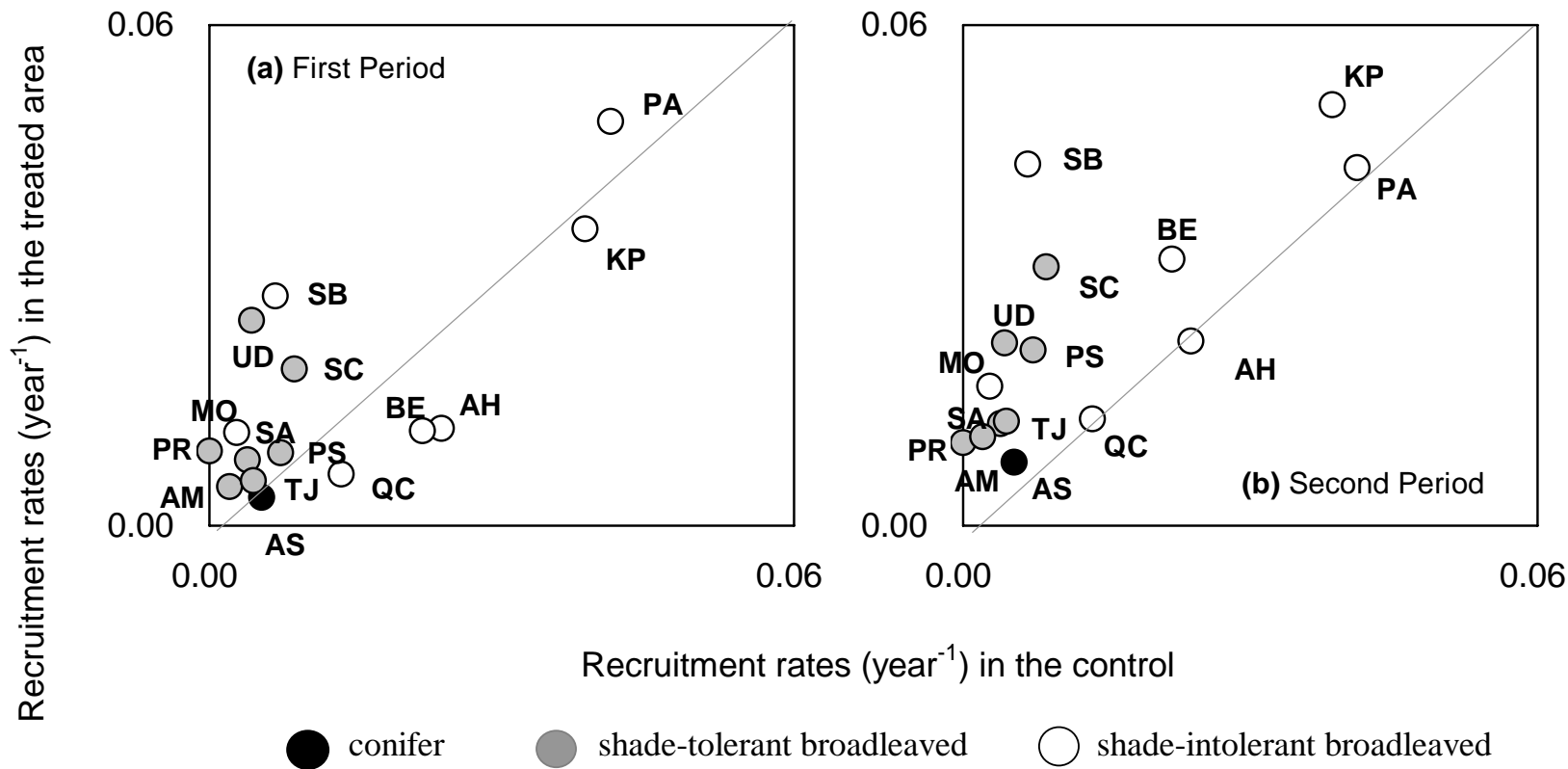
Table 1. Descriptions of the study forest.

Compartment*	Area (ha)	Basal area (m²/ha)			Census year**
		Initial	Harvested (first)	(second)	
5	11.1	27.8	6.8	3.2	1970, 1980, 1990
6	5.6	34.0	4.4	5.7	1971, 1981, 1991
7	8.2	22.6	3.2	4.2	1972, 1982, 1992
8	6.7	27.9	2.9	3.8	1974, 1983, 1993
9	12.9	25.3	5.3	3.4	1976, 1984, 1994
10	17.6	31.4	6.8	4.2	1977, 1985, 1995
subtotal	62.1	28.2	5.4	3.9	-
control	5.9	26.6	0.0	0.0	1979, 1990

* The compartment No.1-4 were not subjected in this study, because their trees were censused without individual identification.

** The census years were in the year before harvesting.

Table 2. Pre-harvest composition of trees with DBH>= 12.5 cm in the study forest.

Species	Abbreviation	Group	Basal area (m²/ha)	(%)	Density (stems/ha)	Maximum DBH (cm)
Abies sachalinensis	**AS**	CF	14.68	49.1	212.9	80
Acer mono	**AM**	BT	3.10	10.4	78.9	70
Tilia japonica	**TJ**	BT	3.06	10.2	50.4	75
Quercus crispula	**QC**	BI	3.06	10.2	33.1	150
Betula ermanii	**BE**	BI	2.17	7.2	27.1	95
Alnus hirsuta	**AH**	BI	0.64	2.1	12.3	75
Magnolia obovata	**MO**	BI	0.56	1.9	16.2	45
Ulmus davidiana	**UD**	BT	0.49	1.6	6.8	80
Ulmus laciniata	**UL**	BT	0.44	1.5	6.0	65
Kalopanax pictus	**KP**	BI	0.28	0.9	3.5	100
Sorbus alnifolia	**SA**	BT	0.23	0.8	6.1	50
Sorbus commixta	**SC**	BT	0.23	0.8	7.3	45
Prunus sargentii	**PS**	BT	0.21	0.7	6.4	45
Phellodendron amurense	**PA**	BI	0.18	0.6	4.8	50
Prunus ssiori	**PR**	BT	0.12	0.4	3.2	50
Betula maximowicziana	**BM**	BI	0.10	0.3	1.0	75
Picea jezoensis,	**PJ**	CF	0.08	0.3	1.0	55
Taxus cuspidata	**TC**	CF	0.07	0.2	1.4	60
Fraxinus mandshurica	**FM**	BT	0.05	0.2	0.9	65
Salix bakko	**SB**	BI	0.04	0.1	1.6	40
Swida controversa	**SW**	BI	0.04	0.1	1.2	45
Picea glehnii	**PG**	CF	0.03	0.1	0.3	55
Betula platyphylla	**BP**	BI	0.02	0.1	0.5	50
Acanthopanax sciadophylloides	**AC**	BT	0.01	0.04	0.4	40
Juglans mandshurica	**JM**	BT	0.01	0.02	0.3	25
Total			29.9	100.0	484	150
Conifer			14.9	49.7	216	80
Shade-tolerant Broadleaved			8.0	26.6	167	80
Shade-intolerant Broadleaved			7.1	23.7	101	150

*CF: conifer, BT: shade-tolerant broadleaved, BI: shade-intolerant broadleaved species. The classification was based on Koike (1987) and Masaki (2002).

Table 3. Changes in basal area during the 20 years period.

| Species | Abbreviation | Group | Basal area (m²/ha) | | | | Recovery (G+R-D) /L |
			logged (L)	grown (G)	recruited (R)	naturally dead (D)	
Abies sachalinensis	**AS**	CF	4.454	5.189	0.286	0.526	1.11
Acer mono	**AM**	BT	1.299	0.521	0.136	0.277	0.29
Tilia japonica	**TJ**	BT	0.842	0.546	0.114	0.127	0.63
Quercus crispula	**QC**	BI	0.689	0.738	0.101	0.118	1.05
Betula ermanii	**BE**	BI	0.803	0.365	0.137	0.052	0.56
Alnus hirsuta	**AH**	BI	0.245	0.157	0.056	0.071	0.58
Magnolia obovata	**MO**	BI	0.248	0.083	0.046	0.034	0.38
Ulmus davidiana	**UD**	BT	0.204	0.143	0.036	0.006	0.85
Ulmus laciniata	**UL**	BT	0.017	0.103	0.009	0.085	1.59
Kalopanax pictus	**KP**	BI	0.049	0.102	0.069	0.006	3.34
Sorbus alnifolia	**SA**	BT	0.094	0.037	0.012	0.012	0.39
Sorbus commixta	**SC**	BT	0.117	0.044	0.032	0.009	0.57
Prunus sargentii	**PS**	BT	0.097	0.026	0.013	0.016	0.24
Phellodendron amurense	**PA**	BI	0.043	0.062	0.093	0.010	3.32
Prunus ssiori	**PR**	BT	0.024	0.026	0.009	0.012	1.00
Betula maximowicziana	**BM**	BI	0.035	0.014	0.013	0.012	0.44
Picea jezoensis,	**PJ**	CF	0.004	0.039	0.003	0.003	9.79
Taxus cuspidata	**TC**	CF	0.013	0.010	0.003	0.002	0.87
Fraxinus mandshurica	**FM**	BT	0.004	0.024	0.016	0.005	9.37
Salix bakko	**SB**	BI	0.010	0.021	0.022	0.005	3.70
Swida controversa	**SW**	BI	0.014	0.010	0.024	0.001	2.36
Picea glehnii	**PG**	CF	0.001	0.012	0.001	0.000	11.92
Betula platyphylla	**BP**	BI	0.002	0.017	0.010	0.004	10.43
Acanthopanax sciadophylloides	**AC**	BT	0.005	0.003	0.002	0.002	0.40
Juglans mandshurica	**JM**	BT	0.002	0.005	0.002	0.001	3.69
Total			9.315	8.296	1.245	1.396	0.87
Conifer			4.471	5.250	0.292	0.532	1.12
Shade-tolerant Broadleaved			2.705	1.477	0.381	0.552	0.48
Shade-intolerant Broadleaved			2.139	1.569	0.571	0.313	0.85

*CF: conifer, BT: shade-tolerant broadleaved, BI: shade-intolerant broadleaved species. The classification was based on Koike (1987) and Masaki (2002).