# Population biology of *Aesculus turbinata* Blume: A demographic analysis using transition matrices on a natural population along a riparian environmental gradient

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**Abstract**

**Population structure and dynamics of a riparian canopy species, *Aesculus turbinata* (Japanese horse chestnut), were analyzed based on the census data collected for the 8 years from 1989 to 1996 in temperate deciduous forests in Ashiu, Kyoto Prefecture, Japan. The censuses were conducted in three permanently established study plots over an environmental gradient that included the lower hill slope, river terrace, and floodplain of a riparian area within a forest stand of approximately 3 ha. Transition matrix based on the data from 1989 to 1996 was provided for the total population made by pooling population data from all subpopulations in three different habitats (i.e. slope, terrace, floodplain). The total *Aesculus* population showed positive population growth ($\lambda=1.0298$). From the elasticity analysis, larger elasticity values were obtained with increasing size- or stage-classes. A combined transition matrix was also constructed for the life-history processes consisting of three subpopulations developed on an environmental gradient. This whole population linked by seed flow showed an increase in population size ($\lambda=1.0286$). The elasticity matrix showed the relative importance of the slope subpopulation, suggesting its significant role as a mainland source population. Log-linear analyses were carried out to examine spatiotemporal variations of life-history parameters; significant effects of stage and plot were recognized, while no effect of year was detected on any life-history parameters except for fecundity.**

*Keywords: Aesculus turbinata*, elasticity, life-history characteristics, population dynamics, riparian forest, transition matrix model.

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## Introduction

The life spans of woody species are exceedingly long, often attaining several hundred years, and thus the age-structure of any single local population can be very complex (Harcombe & Marks 1983; Franklin *et al.* 1987; Peet & Christensen 1987). Because of this, census studies of tree populations are time-consuming and laborious, and it is not easy to obtain a picture of the demographic structure of a local population simply by evaluating the age-structure of a particular species; a somewhat similar situation is also found in long-lived perennial herbs (Kawano 1975, 1985; Kawano *et al.* 1987).

Transition matrix analyses have been used to quantitate various aspects of plant population dynamics of shrubs and trees (Caswell 1989; Silvertown & Lovett Doust 1993b; Silvertown *et al.* 1993), but most previous studies of long-lived species have been conducted on single stands or populations, and the data for several years were often pooled together for analyses (Usher 1966, 1969; Bosch 1971; Hartshorn 1972, 1975; Caswell 1982; Enright 1982; Burns & Ogden 1985; Somarriba 1988; Enright and

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Watson 1992). Studies of this sort only characterize a species over a small portion of the total habitat area where it occurs. Hence, both spatial and temporal census analyses are important because significant aspects of the dynamics of a species will be spatially as well as temporally variable, but such studies have not been conducted until recent years (Franco & Silvertown 1990; on various herbs in Caswell 1989; Nault & Gagnon 1993; Horvitz & Schemske 1995; on shrubs and trees in Namkoong & Roberds 1974; Enright & Ogden 1979; Piñero *et al*. 1984; Platt *et al*. 1988; Martínez-Ramos *et al*. 1989; Bengtsson 1993; Pinard 1993; Alvarez-Buylla 1994; Martínez-Ramos & Samper 1998).

Tree populations often extend over a broad environmental gradient, associated with topographic complexities, and thus transition matrix analyses based on a single stand alone are not sufficient enough to generalize the patterns of population dynamics and demographic structures. This is especially true for riparian species which occur in topographically and edaphically diverse habitats along streams. The vital rates (growth rate, survival rate, and fecundity) may also fluctuate differently in neighboring subpopulations (Namkoong & Roberds 1974; Connell 1978; Enright & Ogden 1979; Piñero *et al*. 1984; Platt *et al*. 1988; Bengtsson 1993; Pinard 1993; Silvertown & Lovett Doust 1993; Alvarez-Buylla 1994; Martínez-Ramos & Samper 1998). The so-called 'Oskar syndrome' is also prevalent in woody species populations (Silvertown 1987). Indeed, recent analyses on the demographic genetic structures of the Japanese beech population revealed the preponderance of specific heterozygote genotypes among the Oskars that have survived under suppressed conditions at the edge of an environmental gradient (Kawano & Kitamura 1997; Kitamura *et al*. 1997a,b).

*Aesculus turbinata* selected is one of the representative riparian elements in Japanese temperate forests. Because it occurs over a wide range of microhabitats within the riparian areas, it seems likely that local subpopulations would have different population dynamics. One of the unique features of riparian habitats is that frequent natural disturbances cause the formation of a mosaic structure of various microtopographical as well as microenvironmental conditions (Gregory *et al*. 1991; Ito & Nakamura 1994; Kaneko 1995). Such differences in background environments may determine the patterns of ecological distribution and the structures of plant populations developed over an environmental gradient from ridge to upper hill slope in non-riparian habitats, and from lower hill slope to terrace and floodplain in riparian habitats (Hiroki 1987; Oshima *et al*. 1990; Yamanaka *et al*. 1993; Sugita *et al*. 1995). Differences in the disturbance regime in the riparian habitats often may cause the patterns of intra- as well as interspecific competition (Alvarez-Buylla & Garcia-Barrios 1993; Oshima & Takeda 1993; Takada & Nakashizuka 1996).

The site-dependent patterns of demographic processes in riparian species likely reflects the local disturbance regime. Physical disturbances by geomorphic processes, for example, such as flooding and landslide may have physically destructive effects on the vital rates of individuals constituting a local population, but at the same time may have beneficial effects on the surviving individuals or on the establishment of seedlings after such disturbances, patches ('gaps') on the forest floor. Therefore, for a riparian species such as *A. turbinata* (hereafter referred to as *Aesculus*) which occurs over an environmental gradient ranging from the slope to the floodplain of a river system, long-term spatial as well as temporal analyses of the demographic processes are necessary in order to understand the effects of disturbance regimes on the maintenance mechanisms of the riparian species population in question.

In the present study, three analyses were conducted. First, in order to monitor spatial and temporal dynamics of *Aesculus* populations we established a permanent plot, and then mapped and marked all horse chestnut individuals within this plot in the Mondoridani river system of Ashiu in Kyoto Prefecture, Japan. Second, based on the census data, transition matrices were prepared for a total population and separately for three subpopulations (i.e. those on the lower hill slope, terrace (high level floodplain), and floodplain (low level floodplain) of the study area (hereinafter called slope, terrace and floodplain subpopulations)). Computations were made of population growth rate ($\lambda$) and elasticity. Third, the patterns of population dynamics of *Aesculus* were assessed via a local population in the Mondoridani based upon all available data.

The questions specifically addressed in this study are as follows: (i) are there significant spatial and yearly differences in demographic parameters such as growth rate, mortality, fecundity, and fate of individuals reflecting all vital rates, among subpopulations developed over an environmental gradient in a riparian habitat; (ii) what are the patterns of population dynamics found in *Aesculus* over the environmental gradient in the riparian habitats (are there any significant dispersal agents for establishment of offspring populations for each subpopulation); (iii) what are the effects of environmental constraints (e.g. differences in the disturbance regime and competition) on different growth stages of individuals in different subpopulations developed in different riparian habitats; (iv) what are the roles of size and density of ecologically empty patches ('gaps') in recruitment and maintenance of subpopulations in different riparian habitats; (v) what are the dynamic changes of *Aesculus* populations in light of the metapopulation concept (Hanski & Gilpin 1997)?

## Materials and methods

### Study species

The Japanese horse chestnut, *A. turbinata* Blume, is the only native species of the Hippocastanaceae in Japan. It occurs primarily in a riparian habitats in cool-temperate forests of Japan (Group for the Study on Ecology of Natural Forests 1972; Miyawaki 1984; Sugita *et al.* 1995). *Aesculus* is a deciduous canopy species that grows to about 30 m in height and 150 cm in diameter at breast height (d.b.h.), and is mainly pollinated by *Bombus hypocrita* and *Bombus ardens* (Kakutani 1994). Fruit set of self-fertilization appears to be low as artificially pollinated trees only produced 4.8% fruits (Taniguchi 1995; Hashizume *et al.* 1996). *Aesculus* is a mast producing species and mast years were observed in 1982, 1987, 1992 and 1997 at around the study area during the 1980–1998 period (on during 1980–1985 in Saito *et al.* 1990; on during 1987–1993 in this study; on 1997–1998 in H. Kawaguchi *et al.*, unpubl. data, 1997–8). Masting interval in Ashiu is approximately 5 years.

Seeds of *Aesculus* are the largest among Japanese species in the cool-temperate forests (mean fresh weight ranged from 9 to 13 g) (Seiwa & Kikuzawa 1991; Taniguchi 1996). Seeds fall by gravity (barochory) in September and October in Ashiu (van der Pijl 1969). Most of the fallen seeds are dispersed by wood mice (synzoochore), mainly *Apodemus speciosus* (Hoshizaki *et al.* 1997; Isaji & Sugita 1997). *Apodemus speciosus* selectively carries seeds of *Aesculus* into gap sites within their home range (Miguchi 1994, 1996). Seeds do not have a dormant period (Nakagoshi 1984) but do not germinate until late April to early June because of low temperatures that follow seed dispersal. *Aesculus* shows a typical hypogeal germination (Schopmeyer 1974). Aggregations of about 20–40 seeds or newly germinated seedlings per site (aprroximately 20 × 20–40 cm) were often observed, they were regarded as collected by wood mice under the $A_0$ layer.

### Study area

The study was conducted in a typical cool-temperate deciduous broad-leaved forest within the Mondoridani mountain watershed (688.7–836.5 m above sea level, 35°20′N, 135°44′E). The watershed (the total watershed area = 16.0 ha) is in the Kyoto University Ashiu Experimental Forest located at the north eastern boundary of Kyoto Prefecture, central Honshu, Japan (Fig. 1). The forests have been intact at least since 1898, and there is no record of human disturbance also before 1898 (Yamanaka *et al.* 1993). The mean annual temperature and precipitation at the weather station (640 m in elevation) in Chojidani, about 2 km from the study area, are 10–11°C and 2895 mm, respectively. Heavy and/or continuous
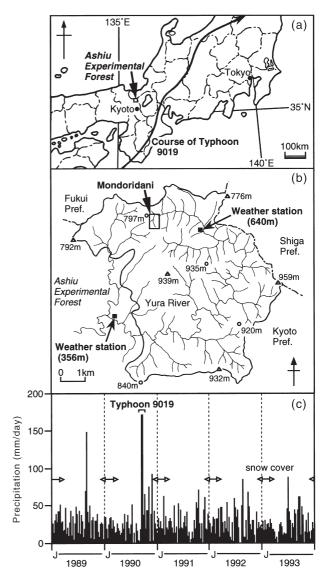


**Fig. 1** Map showing the locations of (a) Ashiu experimental forest and course of typhoon 9019, and (b) the study plot and weather station in Ashiu experimental forest. (c) Daily precipitation at weather station (356 m in elevation) in Ashiu.

precipitations occur occasionally in the monsoon (June to early July) and typhoon season (September to early October). The maximum snowfall is 2–3 m and it occurs between December and February. Soil layers of the study area are primarily Moderately Moist Brown Forest Soils in the Mesozoic and Paleozoic strata (Kyoto University Ashiu Experimental Forest1997).

Vegetation within the riparian zone (Gregory *et al.* 1991; Kaneko 1995) of the old-growth stand above 600 m in elevation is dominated by *Pterocarya rhoifolia* Sieb. et Zucc., *Aesculus turbinata* Blume, *Quercus mongolica* var. *grosserrata* (Blume) Rehder et Wilson, and *Fagus crenata* Blume (Miyawaki 1984). *Aesculus turbinata* and *Pterocarya rhoifo-*

*lia* are both dominant tree species in the cool-temperate riparian forests of Japan. Earlier vegetation studies of the Mondoridani valley have demonstrated that there occur unique ecological distributions of woody species over an environmental gradient, forming a continuum that consists of several predominant species, such as *Pterocarya rhoifolia*, *Acer nipponicum*, *Aesculus turbinata*, *Quercus mongolica* var. *grosseserrata*, *Fagus crenata* and *Cryptomeria japonica* var. *radicans* (Group for the Study on Ecology of Natural Forests 1972; Oshima *et al.* 1990; Yamanaka *et al.* 1993; also see Table 1). On the floodplain of the river, *Pterocarya rhoifolia*, an extremely moisture-tolerant species, is predominant accompanying various riparian elements of herbs and ferns on the forest floor; from the terrace to the lower hill slope on the topographically continuous extension from the floodplain, *Aesculus turbinata* and *Quercus mongolica* var. *grosseserrata* are predominant, often accompanying a thick understory of the dwarf bamboo, *Sasa senanensis*, on the forest floor. However, from the upper hill slope to the ridge the canopy layer trees are gradually replaced by the Japanese beech, *Fagus crenata*, and the Japanese cedar, *Cryptomeria japonica* var. *radicans*, both representative temperate forest elements in Japan.

## Methods

*Valley topography and edaphic conditions.* Because the study area was a mosaic of landform surfaces, we divided into three habitats based on topography: (i) slope; (ii) terrace; (iii) floodplain (Fig. 2). Flooding frequently disturbs the floodplain habitats. The slope habitat consists of toe and lower hill slopes, and the average gradient of the slope habitats is 30°–50°. The terrace habitat is high-level floodplain of a valley floor and often occurs between the floodplain and slope habitats. It is characterized by flat small terrace surface with soils that are greater than 50 cm in thickness (Table 1).

In November 1989, we determined the soil types and its characteristics at five sites on the floodplains, four sites on the terraces, and four sites on the slopes. Soil samples of A and B layers in soil were collected using a sampling core ($20 \times 20 \times 10$ cm), and the moisture contents were calculated based on fresh and dried weight for each sample. There were patchy distributions of extremely wetted types of brown forest soils (wet brown forest soil and slightly wetted brown forest soil according to Kawada (1989)) on the floodplain along the stream (Table 1).

**Table 1** Vegetation, environmental conditions, gap and disturbance properties on the three habitats within the 2.75 ha study plot

|  | Floodplain | Terrace | Slope |
|---|---|---|---|
| Study area (ha, %) | 0.34 (12.4%) | 0.53 (19.3%) | 1.88 (68.4%) |
| Density of stems > 10 cm d.b.h. (no./ha) | 155.9 | 122.6 | 277.0 |
| Total basal area of stems > 10 cm in d.b.h. (m²/ha) | 12.8 | 15.4 | 26.2 |
| No. tree species > 10 cm in d.b.h. | 11 | 18 | 36 |
| Dominance of major tree species (% of total BA/% of total no.) |  |  |  |
| *Pterocarya rhoifolia* | 83.1/64.2 | 0.3/1.5 | 0.0/0.0 |
| *Acer nipponicum* | 7.8/13.2 | 1.2/4.6 | 0.6/1.3 |
| *Aesculus turbinata* | 0.2/1.9 | 44.0/13.9 | 7.3/2.7 |
| *Quercus mongolica* | 0.0/0.0 | 25.7/6.2 | 10.9/3.8 |
| *Fagus crenata* | 2.5/1.9 | 17.2/23.1 | 34.4/28.8 |
| *Cryptomeria japonica* var. *radicans* | 0.0/0.0 | 1.8/6.2 | 27.3/27.9 |
| Dominant species on forest floor | *Arachniodes standishii* | *Sasa senanensis* | *Arachniodes standishii* |
|  | Various herbs | Shrubs | *Hydrangea paniculata* |
| Mean relative light intensity* (%) (mean ± 1SE min.–max.) | 7.13 ± 0.47 (0.97–24.4) | 5.91 ± 0.58 (0.93–18.1) | 5.31 ± 0.48 (0.94–35.2) |
| Type of forest soil | Wet (slightly wetted) brown forest soil | Moderately moist brown forest soil | Moderately moist brown forest soil |
| Mean depth of A and B layers of soil (cm) (mean ± 1SE) | 42.0 ± 4.9 | 52.5 ± 2.5 | 50.0 ± 2.0 |
| Total gap area (% of each site) | 29.8 | 14.6 | 11.7 |
| Mean gap size (m²) (mean ± 1SE, min.–max.) | 145.7 ± 69.0 (11.6–388.6) | 120.9 ± 43.9 (14.2–268.8) | 99.6 ± 15.9 (2.4–549.5) |
| Density of gaps (no./ha) | 14.8 | 9.5 | 34.6 |
| Major disturbance agents |  |  |  |
| Agents of geomorphic disturbance processes | Flooding | None | Landslide |
| Order of geomorphic disturbance frequency | $10^0 \sim 10^1$ year | $10^2$ year | $10^0 \sim 10^2$ year |
| Agents of other physical disturbances | Treefall/branchfall | Treefall/branchfall | Treefall/branchfall |

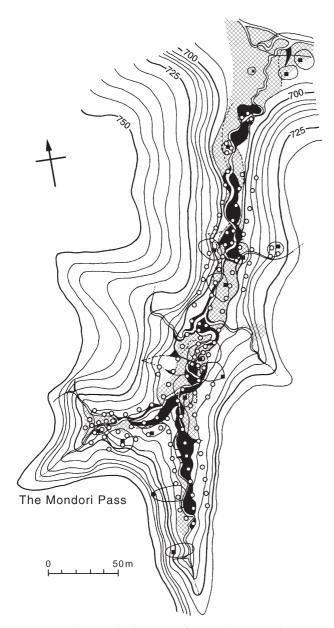*% of the light intensities under a canopy per the light intensities in a open site.

**Fig. 2** Map showing the locations of 130 seed traps, and crowns of mature trees on the three habitats based on topography: slope, terrace, and floodplain. ■, mature tree; ○, seed trap; ●, floodplain; ⊚, terrace; ○, slope. Scale, 50 m.
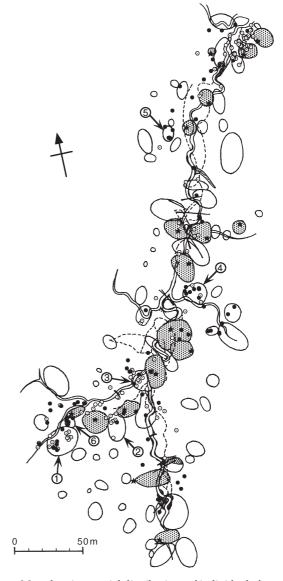


**Fig. 3** Map showing spatial distributions of individuals for each growth stage, crowns of mature trees, and treefall gaps in 1992. Arrows indicate the gaps in which *Aesculus* juveniles were aggregated; the numbers accompanying the arrows are also used in Fig. 14. Dotted lines show past channels, and oblique areas show where landslides occurred due to the typhoon 9019 in 1990. ○, established seedlings (S); ⊙, monopodial juveniles (J₁); ●, branching juveniles (J₂); ★, mature trees (M); ▨, crown of mature tree; ○, gap area. Scale, 50 m.

*Vegetation dynamics and gap properties.* In 1989, a 2.75-ha permanent plot covering the three habitats within the riparian area was established. The grid included 63 plots (10 × 10 m). In 1991, the 63 study plots were divided into subplots (5 × 5 m), and the distributions of crowns of mature trees were recorded for each subplot. In 1992, a 16.0-ha permanent plot covering the whole Mondoridani watershed was established. All living and dead tree species above 10 cm in d.b.h. were tagged and mapped, and calculated dominance of each major canopy species (Table 1).

The distributions of canopy gaps (= areas where the height of regeneration canopy layer is below 10 m, according to Yamamoto (1992)) were examined within the 16.0-ha plot (Yamanaka *et al.* 1993; Yamanaka *et al.* 1997; see also Table 1 and Fig. 3). The light intensities on the forest floor were measured with a radiometer (MINOLTA, Osaka Japan Illuminance meter, T-1H) at each corner of every subplot at 1.3 m height in July 1992, and then

relative light intensity (% of the light intensities under a canopy per the light intensities in a open site) was calculated for each measured plot (Table 1).

*Seed production and dispersal.* Seed production between 1990 and 1993 was studied by placing 130 seed traps (0.25 m² in size) at the four corners of each the 63 plots established in 1991 (Fig. 2). Seeds were collected from seed traps monthly during the dispersal period. The recruitment proportions of total viable seeds dispersed into each habitat by barochory from mature trees on the slope and terrace habitats, respectively, were calculated based on the total number of viable seeds trapped on each habitat.

*Seedling dynamics.* To study the fate of current-year seedlings in 1991, 1992 and 1993, 102 quadrats (1×1 m) located near each seed trap were established at regularly 10 m intervals in 1990 (Fig. 2). In addition, 51 subplots (5 ×5 m) were also located around mature trees in 1991. The current-year seedlings were tagged and their fates (i.e. growth, degrees of damages by herbivores and diseases, and mortality) were recorded at weekly intervals from April through July, and at monthly intervals from August through December after the growing season.

*Tree growth.* All horse chestnut individuals present as established current-year seedlings, juveniles, and mature trees within the 2.75 ha plot were labeled and mapped in 1989. Their status (normal, damaged or dead) was recorded annually at the end of each growing season. They were also measured annually for main stem length, diameter at breast height and/or ground level, and the number of winter buds and branches per individual. Ages of individuals were estimated based on the number of winter bud scales for juveniles below 5 cm in d.b.h., and on the number of annual rings on core samples for individuals above 5 cm in d.b.h. A field-scope (Nikon, Tokyo, Japan, Field Scope ED) and a measuring camera (MINOLTA MC-100) were used in measuring the annual height increments for individuals above 4 m in height. Demographic censuses were conducted for the 4 years 1989 through 1992, and again in 1996 and 1997 for individuals that exceeded 4 m in height and >5 cm in d.b.h. A total of 1347 individual samples were recorded (755 individuals at the slope, 432 at the terrace, 160 at the floodplain) during the census period.

*Tree mortality.* Marked plants were examined seasonally to determine if they had been damaged or had died. Causes of death or damage were classified according to Harcombe and Marks (1983), Franklin *et al.* (1987), Peet and Christensen (1987), and Kaneko (1995). Causes of death or damage were divided broadly into three categories based on disturbance regime: (i) physical distur-bances by geomorphic processes (individuals were uprooted, broken stems, washed away, and buried in the deposits by flooding or landslides, hereinafter called geo-morphic disturbances); (ii) physical disturbances by other causes rather than geomorphic disturbance processes (fallen or broken stems due to strong wind, snowfall, snowcreep, treefall, branchfall, etc., hereinafter called physical disturbances); and (iii) biotic and environmental stresses (standing death, predation by herbivores, pathogen attack, drought, overtopping and shading of the other tree species or dwarf bamboos, hereinafter called environmental stresses).

*Demographic analyses.* For the analyses of life-history processes, four size-class categories were based on the length of the main stems (L); class I = L < 1.0 m, class II = $1.0 \leq L < 4.0$ m, class III = $4.0 \leq L < 16.0$ m, class IV = $16.0 \leq L$. Four developmental phase classes were: 1, current-year seedlings established in autumn (S); 2, monopodial juve-niles ($J_1$); 3, branching juveniles ($J_2$); and 4, mature trees (M). The analyses of vital rates and the projection matrix analyses were based on seven stage-classes, combinations of size and phases: 1 = S-I (S), 2 = $J_1$-I, 3 = $J_1$-II, 4 = $J_2$-I, 5 = $J_2$-II, 6 = $J_2$-III, and 7 = M-IV (M) (Fig. 4).

Replicated goodness-of-fit tests were used to determine whether there were differences in mortality rates between stages and between habitats (Sokal & Rohlf 1995). One-way ANOVA was used to detect whether differences in growth and relative growth rates existed between stages and between habitats.

*Log-linear analyses.* To determine whether mortality and damage varied across space and over time, log-linear analyses were carried out (as in Caswell 1989; Sokal & Rohlf 1995; on plant species in Platt *et al.* 1988; Bengtsson 1993; Nault & Gagnon 1993; Pinard 1993; Horvitz & Schemske 1995). Categorical response variables were plot (three habitat plots), stage (seven stage classes in year *t* as described), mortality and damage (four categories: (i) sur-vival, death or loss due to (ii) geomorphic; (iii) physical disturbances; and (iv) environmental stresses) and year (three transition periods: 1989–1990, 1990–1991 and 1991–1992). We examined each period individually, considering the effects of plot and stage on mortality and damage during that transition period; each stage individually, considering the effects of year and plot at that stage; and each plot individually, considering the effects of year and stage for that plot. These analyses were based on a three-way contingency table for each transi-tion period, each stage, or each plot. The log-likelihood statistics were obtained, adding 0.5 to all cells to avoid estimation problems for cells with zero observations (Fin-gleton 1984).
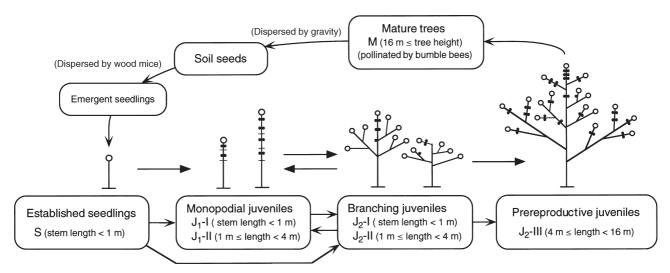
**Fig. 4** Diagram illustrating the steps in growth stages of juveniles (from seedlings to monopodial, branching and prereproductive juveniles) of *Aesculus*. ○, apical winter bud; ●, lateral winter bud.

Log-linear analyses were also carried out to determine whether the fates of individuals varied through space and time (as in Caswell 1989; Bengtsson 1993; Horvitz & Schemske 1995; Sokal & Rohlf 1995). In these analyses, we set the future status of individuals (S, $J_1$–I, $J_2$–I, $J_1$–II, $J_2$–II, $J_2$–III and M, and dead) in the succeeding year as fates. Fates of individuals are integrated parameters which reflect all population processes and vital rates (fecundity and recruitment process, survival including stasis and retrogression, and growth processes). These analyses were based on a three-way contingency table for each transition period, each stage, or each plot.

*Matrix analyses.* Stage-classified projection matrices were made: the first matrix was developed by pooling population data from all three subpopulations, based on the data from 1989 to 1996. Fecundity was calculated as the observed number of established seedlings per mature tree. No individual at the M stage died during 1989–1998. We estimated survival probability values for the M stage based on census data on the growth rate of d.b.h. for each subpopulation.

Matrices were made separately for each subpopulation in three different habitats (i.e. slope, terrace, floodplain) based on the data for all the transition periods 1989–1996. After examining the spatial effects on the fates of each life-history stage by log-linear analysis, we constructed a flow diagram of the life-history processes of three *Aesculus* subpopulations based on the census data, and incorporated the possible seed dispersal links among three subpopulations based on the seed trap data (Fig. 5). Based on Fig. 5, we combined these matrices of the three subpopu-

lations and analyzed their dynamics. This projection matrix for the whole population consisted of the three subpopulations and it was developed in order to analyze the maintenance mechanisms of each subpopulation and to assess the role of each subpopulation in the dynamic processes of the total population. Fecundities at each habitat were calculated based on the proportions of observed numbers of established seedlings per mature tree.

Matrices were used to calculate the finite rates of increase, λ (Caswell & Werner 1978). Elasticity analyses were also conducted based upon those matrices (de Kroon *et al.* 1986).

## Results

### Population structure and ecological distribution

*Aesculus* was abundant in the slope and terrace habitats, where the subpopulations contained plants in all size and phase categories (Oshima *et al.* 1990). The proportions of plant in each subpopulation during 1989–1992 averaged 63.2%, 25.9% and 10.9% on the slope, terrace, and floodplain sites, respectively (Fig. 6a). However, *Aesculus* was the dominant canopy species in the terrace habitats while it was not dominant in the slope habitats (Table 1). Class III and IV plants were more abundant on the terrace sites (35.6/ha) than slope sites (27.8/ha). Densities of class I and II plants were higher on the slope (222.8/ha) than the terrace sites (172.9/ha) (Fig. 6b). Mean and maximum d.b.h. of mature trees were greater on the terrace (85.7/149.8 cm) than the slope sites (75.3/98.5 cm).

**Fig. 5** Flow diagrams illustrating the life-history processes of *Aesculus* population, assuming three subpopulations linked by seed flow among subpopulations.

*Population processes and demographic changes*

*Spatial and yearly changes in recruitment processes.* During the study period, all individuals > 30 cm in d.b.h. flowered and produced fruits. More than 80% of mature trees produced seeds in all years; the mean annual number of viable seeds per fruiting tree ranged from 356 to 1157 (Table 2). The number of viable seeds (mean ±1SE) produced by mature trees above 80 cm in d.b.h. (1006 ± 308) was about twice the number produced by trees between 30 and 80 cm in d.b.h. (486 ± 130) (*t*-test, $0.05 < P < 0.1$). Because of this trend, the mean number (mean ±1SE) of viable seeds during 1990–93 was greater in the terrace subpopulation (839 ± 282) than in slope subpopulation (600 ± 240).

A mean 65.4% of the seeds produced by trees on slope sites remained in that habitat. The majority of seeds (71.1%) produced on the terrace sites were dispersed to floodplain sites (Table 2). The temporal trends in the recruitment proportions of total viable seeds depended only on the locations (the distances from adjacent other type of habitats) of mature trees that produced seeds in that year since seeds dispersed by barochory.

There were significant differences (Kolmogorov-Smirnov test, $P < 0.001$) between frequency distributions of seeds and current-year seedlings recruited into each habitat (Fig. 7). There were considerable numbers of seedling quadrats on the slope habitats in which current-year seedlings emerged in spring instead of no recruited

seeds in their adjacent seed traps in previous year. This indicated that these seedlings on the slope habitat were dispersed by not barochory but synzoochore.

Survival rates from viable seed fall to seedling establishment were significantly low at the floodplain and significantly high at the slope habitat (Fig. 8). Mean survival rates of seeds from falling to germination were higher on the slope (12.5%) than the terrace (9.5%) and floodplain (2.9%) habitats. Mean survival rates of current-year seedlings from germination to establishment were also highest on the slope (45.9%) compared to the terrace (29.9%) and floodplain (33.9%) habitats. Percentages of deaths caused by leaf or stem predation of all current-year seedlings ranged from 40.0 to 49.4%, and there were no difference among habitats. Percentages of standing death due to shading or drought among all mortality factors were higher on the terrace and floodplain (50.0 and 56.0%) than the slope (32.5%) habitat.

*Spatial patterns of growth parameters.* Demographic censuses revealed size-dependent growth, branching and flowering patterns (Fig. 9). In size-classes I and II, both monopodial and branching plants were found. However, the proportion of plants in the monopodial stages (S and $J_1$) decreased as the stem length increased. In the total population, 96.8% of individuals in size-class I were monopodial, and 68.9% of individuals in size-class II were branching. In size-classes III and IV, all individuals were
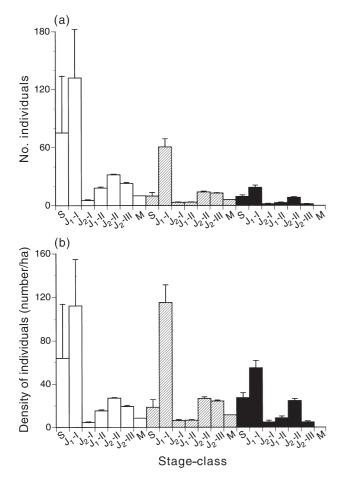
Fig. 6 (a) Stage-class distribution over the three habitats. Percentages of total number in each subpopulation are shown in parentheses: □, slope (63.2%); ▨, terrace (25.9%); ■, floodplain (10.9%). (b) Density of individuals at each of three habitats. Total density of each subpopulation are shown in parentheses: □, slope (249/ha); ▨, terrace (209/ha); ■, floodplain (140/ha). Values are means of stage-classes during 1989–1992, and vertical lines indicate +1 SE.
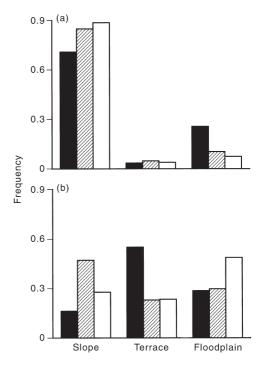


Fig. 7 Comparisons among the frequency distributions of the vital seeds recruited on the ground, and the emergent and established seedlings in the succeeding year on the three habitats. (a) The case from 1990 to 1991 that is an example of a masting year for a mature tree on the slope. (b) The case from 1991 to 1992 that is that for a mature tree on the terrace. ■, viable soil seeds; ▨, emergent seedlings; □, established seedlings.

Table 2 Yearly changes in seed production, and the recruitment proportions (%) of total viable seeds that dispersed by barochory based on the data in 130 seed traps on each of three habitats during 1990–1993

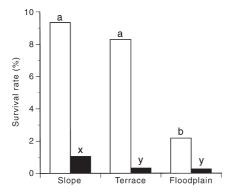|  | 1990 | 1991 | 1992 | 1993 | Mean±1SE |
|---|---|---|---|---|---|
| No. mature trees produced seeds (/ha) | 6.37 | 6.37 | 7.35 | 7.35 | 6.86±0.28 |
| % of mature trees produced seeds | 81.3 | 81.3 | 93.8 | 93.8 | 87.5±3.61 |
| No. viable mature seeds (/ha) | 2268 | 4333 | 8499 | 4427 | 4882±1305 |
| No. viable seeds per mature trees produced seeds | 356 | 681 | 1157 | 603 | 699±168 |
| Dispersal proportions by barochory (%) | | | | | |
| From mature trees in the slope | | | | | |
| Slope sites | 94.9 | 46.5 | 89.0 | 31.3 | 65.4±15.7 |
| Terrace sites | 5.1 | 10.1 | 5.5 | 34.3 | 13.8±6.96 |
| Floodplain sites | 0.0 | 43.4 | 5.6 | 34.3 | 20.8±10.6 |
| From mature trees in the terrace | | | | | |
| Slope sites | 0.0 | 0.0 | 0.0 | 0.0 | 0.0±0.0 |
| Terrace sites | 0.0 | 67.5 | 41.1 | 6.9 | 28.9±15.7 |
| Floodplain sites | 100.0 | 32.5 | 58.9 | 93.1 | 71.1±15.7 |

**Fig. 8** Survival rates from seed fall by barochory to establishment in next autumn for each subpopulation. The results were the cases from 1990 to 1991 (□) and from 1991 to 1992 (■) in 130 sets of seed traps and seedling quadrats. Bars sharing letters within either group are statistically indistinguishable ($P < 0.05$).
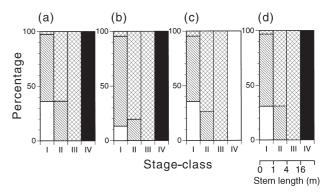


**Fig. 9** Relationships between size- and stage-classes during 1989–92 for (a) slope, (b) terrace, (c) floodplain subpopulation and for (d) the total pooled population. □, established seedlings (monopodial, S); ▨, monopodial juveniles ($J_1$); ▨, branching juveniles ($J_2$); ■, mature trees (M).

at the branching ($J_2$) and mature (M) stages, respectively. These trends were similar at all three habitats; slope, terrace, and floodplain, but there was no mature plant in floodplain subpopulation (Fig. 9).

There was significant variation in growth rates (GR) and relative growth rates (RGR) of stem length among stage-classes (Fig. 10). $J_2$-III stage had the significantly largest GR, followed by $J_2$-II and M; GR was significantly low for S stage (Fig. 10a). While S stage had the significantly largest RGR, followed by individuals in size-class I, RGR was significantly low for stage-class M (Fig. 10b).

There was no significant variation in GR and RGR among topographic habitats except for GR of S stage (Fig. 11). GR of S stage was significantly lower on the slope habitats than the terrace habitats (Fig. 11a).

*Spatial and temporal patterns of mortality.* Based on the results of log-linear analyses, there was no significant effect of stage at the floodplain, but stage had a significant effect at the slope and terrace (Table 3a). Log-linear analyses of mortality and damage for each site in its entirety showed no significant effect of year (Table 3b). Log-linear analyses of mortality and damage for each stage showed that there was no significant effect of year for all stages except for S and $J_1$-I. Since a major typhoon attacked the study area in 1990, various geomorphic disturbances, such as flooding, bank undercutting and landslide, occurred in the study area due to this typhoon. Mortality and damage rates at the S and $J_1$-I during 1989–90 (typhoon year period) was higher than those during the other normal year periods (1990–1991 and 1991–1992). There were significant effects of plot for S, $J_1$-I, $J_2$-I and $J_2$-II stages (Table 3c).

There were significant differences in mortality and damage rates between stage-classes, reflecting localized layer structures of forest (Fig. 12). Mortality rate was highest at S stage and decreased with increase in stem length. Mortality rates at $J_1$-II, $J_2$-II, $J_2$-III and M stages were significantly lower than those for S and $J_1$-I stages, while damage rates were significantly high at $J_2$-II, $J_2$-III and M stages than other smaller stages (Fig. 12).

Mortality and damage rates varied significantly between habitats, because of localized disturbance regimes of that habitat (Fig. 13). Mortality and damage rates were higher on the floodplain and terrace than on the slope for all stages except for $J_2$-III stage. The composition of causes of mortality or damage would be different among the three topographic habitats. There was almost no death and loss caused by geomorphic disturbances at the slope for all stage-classes (Fig. 13).

Mortality and damage rates for each stage also showed site-dependent patterns (Fig. 13). For the S stage, this rate was significantly higher in the terrace and floodplain sites than slope habitats. Mortality and damage rates at the S stage at the terrace habitats were due mainly to physical disturbances (individuals were fallen or broken stems due to treefall, branchfall, snowfall, strong wind, etc.), or environmental stresses (individuals died standing or by predation, pathogen attack, drought, overtopping and shading of the other tree species or dwarf bamboos). Those rates in the floodplain habitats were due mainly to geomorphic disturbances (individuals were uprooted, broken stems, washed away, buried in the deposits by geomorphic processes such as flooding and erosion, etc.). For the $J_1$-I stage, mortality and damage rates were significantly higher at the floodplain than at the slope and terrace habitats. Mortality at $J_1$-I stage was due to geo-
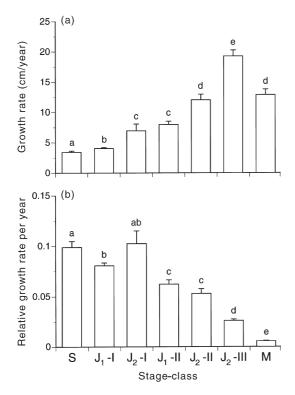
**Fig. 10** Relationships between stage-classes and (a) growth rate (cm/year) and (b) relative growth rate (/year) of stem length. Values are averages of stage-classes during the study period and vertical lines indicate +1SE. These growth rates are calculated based on growth data for normal individuals which survived without damage during each transition period. Significant differences ($P < 0.05$) among stage-classes are indicated by different letters above the bars. Sample sizes: S = 147, $J_1$-I = 490, $J_2$-I = 29, $J_1$-II = 95, $J_2$-II = 204, $J_2$-III = 192, and M = 112.

**Fig. 11** (a) Growth rate (cm/year) and (b) relative growth rate (/year) of stem length for each subpopulation: slope (□), terrace (▨), and floodplain (■). Values are averages of stage-classes during the study period and vertical lines indicate +1SE. These growth rates are calculated based on growth data for normal individuals which survived without damage during each transition period. Significant differences ($P < 0.05$) among subpopulations are indicated by different letters above the bars. Sample sizes of each stage for three habitats: S = 147, $J_1$-I = 490, $J_2$-I = 29, $J_1$-II = 95, $J_2$-II = 204, $J_2$-III = 192, and M = 112.

morphic disturbances at the highest rate for the floodplain (Fig. 13). At the $J_1$-II stage, no significant difference was detected in mortality and damage rate between habitats. For the $J_2$-I, $J_2$-II and $J_2$-III stages, mortality and damage rate was significantly higher on the floodplain habitat than on the slope or terrace habitats. Mortality of $J_2$-I was caused mainly by physical disturbances on the floodplain (Fig. 13). Mortality and damage rates at $J_2$-II and $J_2$-III stages were caused due mainly to both physical and geomorphic disturbances in the floodplain (Fig. 13).

*Log-linear analyses on fates of individuals.* Log-linear analyses of the fates of individuals in each plot showed a significant effect of stage. There was no significant year effect for terrace and floodplain habitats but a significant effect of year on the slope (Table 4a). Log-linear analyses of the fate of individuals during each period showed significant effects of stage and plot (Table 4b). In log-linear
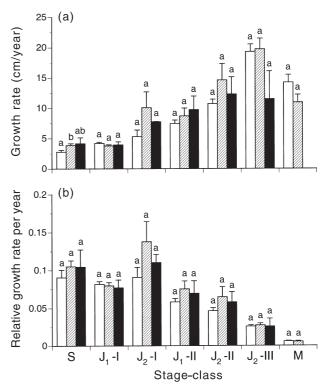
analyses at each stage, we found that plot significantly affected transitions at two stages (S and $J_1$-I) and that year had no significant effect on the fate in any individuals except for those at M stage (Table 4c). This fate of M stage meant the number of established seedlings per mature tree during each period (= fecundity).

*Matrix analyses*

λ-*values and spatial differences in transition probability.* The total *Aesculus* population showed an increase in size (λ = 1.0286) when data over an 8-year period (1989–1996) from all topographic habitats were pooled (Table 5). The projection matrix for a pooled population showed that staying in the same stage was the most probable event for survivors at the juvenile and mature stages. Comparing the survival rates of each size-class, $J_2$ stage showed higher percentage survival rates than $J_1$ stage (Table 5).

**Table 3** Results of log-linear analyses on mortality and damage (Three-way). (a) The effects of year and stage on mortality and damage at each plot, (b) the effects of plot and stage during each period, (c) the effects of year and plot for each stage

| (a) Plot | Year | Stage |
|---|---|---|
| Slope | 5.91[NS] | 47.69*** |
| Terrace | 4.52[NS] | 44.55*** |
| Floodplain | 9.71[NS] | 13.39[NS] |
| (b) Period | Plot | Stage |
| 1989–1990 | 35.09**** | 52.10**** |
| 1990–1991 | 21.42** | 25.31[NS] |
| 1991–1992 | 23.15*** | 22.60[NS] |
| (c) Stage | Year | Plot |
| S | 12.61* | 40.48**** |
| $J_1$-I | 17.05** | 29.49**** |
| $J_2$-I | 2.60[NS] | 14.32*** |
| $J_1$-II | 2.61[NS] | 5.23[NS] |
| $J_2$-II | 6.32[NS] | 20.39** |
| $J_2$-III | 5.52[NS] | 11.31[NS] |
| M | 1.26[NS] | 7.77[NS] |

In these analyses, the categorical response variable, mortality and damage was divided into four categories: (i) survival, death +loss from (ii) geomorphic disturbances; (iii) physical disturbances; and (iv) environmental stresses. The incremental $G^2$ and whether mortality and damage are statistically different among sources of variable or not, are indicated using symbols. NS, not significant; * $0.01 \leq P < 0.05$; ** $0.001 \leq P < 0.01$; *** $0.0001 \leq P < 0.001$; **** $P < 0.0001$.
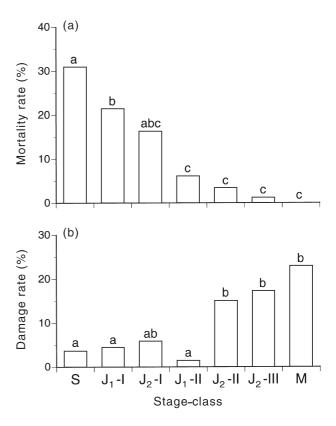


**Fig. 12** Relationships between stage-classes and (a) the mortality and (b) damage rate during the study period. The number alive at the beginning of the seasons: S = 364, $J_1$-I = 560, $J_2$-I = 49, $J_1$-II = 81, $J_2$-II = 203, $J_2$-III = 165, and M = 121. Bars sharing letters are statistically indistinguishable ($P < 0.05$).

Considering all the circumstantial evidence of demographic changes in each subpopulation, and modes of propagule recruitment and dispersal, the matrix analysis for a whole population was conducted (Table 6a). The whole population showed an increase in size ($\lambda = 1.0298$), although the floodplain subpopulation included no mature plants and seeds are always dispersed from the adjacent terrace and/or slope subpopulations.

Environmental conditions of the habitats, including topography, are often critical for certain growth stages of *Aesculus*. The slope habitat was most favorable for survival of S, $J_1$-I, $J_2$-I and $J_2$-II stages, but the terrace habitat was better for the survival of $J_2$-III. Not only was the survival rate at each stage affected by the plot, but also the fate of individuals differed among different stage-classes. Some individuals proceed to the next growth stage, but others stayed the same or returned to the previous stage (Table 6a). Compared to the slope habitat, the terrace is obviously much more favorable for the growth of the $J_2$-III to M stage. On the slope, all survivors at S stage proceeded to the $J_1$-I stage, but on terrace and floodplain, some survivors at S stage proceeded to the $J_2$-I stage. The fates of $J_2$-I juveniles also varied among the

sites. On the slope 83.3% of the survivors stayed in the $J_2$-I stage, while on the terrace 50% of the survivors regressed to the $J_1$-I stage. Regression to the $J_1$-I stage means that the individuals were often forced to survive at that stage under such high mortality risk.

*Spatial differences in elasticity values.* The elasticity matrix for a pooled population indicates that survival parameters, especially the survival probabilities for the larger stages (M, $J_2$-III, and $J_2$-II) contributed more to the population growth rate ($\lambda$) than other parameters (Table 5). Maintaining a mature tree that can produce seeds seems to be the most important for population maintenance. Fecundity had little impact on the population growth rate.

Furthermore, the elasticity matrix for a whole population showed the relative importance of the slope subpopulation, suggesting its significant roles as the main source of offspring recruitment over an environmental gradient developed across the river system. The elasticities of the floodplain subpopulation was equal to zero (Table 6b).
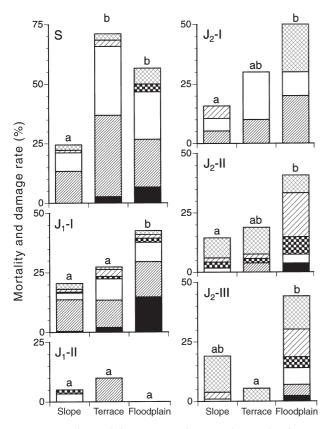
**Fig. 13** Mortality and damage rates due to each mortality factor; physical disturbances by geomorphic processes, physical disturbances by other causes, and biotic and environmental stresses, on each three habitats during the study period. Sample sizes of each stage for three habitats: S = 388, $J_1$-I = 560, $J_2$-I = 49, $J_1$-II = 81, $J_2$-II = 203, $J_2$-III = 165, and M = 121. ■, mortality (geomorphic disturbances); ▨, mortality (physical disturbances); □, mortality (environmental stresses); ▨, damage (geomorphic disturbances); ▨, damage (physical disturbances); ▨, damage (environmental stresses). Bars sharing letters are statistically indistinguishable ($P < 0.05$).

**Table 4** Results of log-linear analyses on fates of individuals (Three-way). (a) The effects of year and stage on fates at each plot, (b) the effects of plot and stage during each period, (c) the effects of year and plot for each stage.

| (a) Plot | Year | Stage |
| --- | --- | --- |
| Slope | 64.01**** | 820.09**** |
| Terrace | 11.52[NS] | 395.54**** |
| Floodplain | 4.12[NS] | 207.35**** |
| (b) Period | Plot | Stage |
| 1989–1990 | 27.37* | 467.49**** |
| 1990–1991 | 36.17** | 550.93**** |
| 1991–1992 | 41.02*** | 473.77**** |
| (c) Stage | Year | Plot |
| S | 13.53[NS] | 47.67**** |
| $J_1$-I | 6.08[NS] | 33.13** |
| $J_2$-I | 2.92[NS] | 7.76[NS] |
| $J_1$-II | 2.80[NS] | 14.19[NS] |
| $J_2$-II | 1.65[NS] | 8.10[NS] |
| $J_2$-III | 0.59[NS] | 17.66[NS] |
| M | 56.06**** | 22.76[NS] |

In these analyses, we set the future status of individuals (S, $J_1$-I, $J_2$-I, $J_1$-II, $J_2$-II, $J_2$-III, M and dead) in the succeeding year as fates. The incremental $G^2$ and whether fates (to which status individuals would make transition) are statistically different among sources of variable or not, are indicated using symbols. NS, not significant; * $0.01 \leq P < 0.05$; ** $0.001 \leq P < 0.01$; *** $0.0001 \leq P < 0.001$; **** $P < 0.0001$.

gap site showed similar patterns, because patch populations may consist of cohorts that were established in the same season (Fig. 14b).

## Discussion

In order to understand the mechanisms of population dynamics and demographic substructure of a particular species, including competitive interactions with other woodland elements, it seems very important to cover the range of ecologic distribution of a particular plant species population in the study area, since population behaviors may be different in different parts of the habitats. What we have asked in this study is, first, whether or not there are any significant spatial differences in demographic parameters, such as vital rates (growth rates, mortality and fecundity), and fate reflecting all vital rates among three different subpopulations established on the floodplain, terrace, and slope over an environmental gradient of a riparian habitats; and, second, what the relationships are between spatial and over-time changes in these demographic parameters. The results of the present long-term demographic studies and matrix analyses on the three study plots of *Aesculus* provided a great deal of new evi-

*Gap properties in each subpopulation*

In the floodplain sites, there were a few large gaps made by the falling of large trees. The percentage of total gap areas to the total study area was highest on the floodplain. In contrast, there were many smaller gaps in the slope sites, and the percentage of total gap areas was low (Table 1).

Most individuals in smaller gaps remain in the smaller and younger stages (Fig. 14). Patch populations in large treefall gaps mainly consisted of stage-classes $J_1$ and $J_2$ (Figs 3 and 14a). Such patch populations in gap sites were prevalent on both the slope and terrace, but were not found on the floodplain (Fig. 3). These facts indicate that gap sites on the slope and terrace are possibly safe sites for *Aesculus*. Furthermore, age-class distributions of each

**Table 5** The projection and elasticity matrices for a total population made by pooling population data from all three subpopulations in the study plot

| Stage-class at year $t+1$ | S | $J_1$-I | $J_2$-I | $J_1$-II | $J_2$-II | $J_2$-III | M |
|---|---|---|---|---|---|---|---|
| | | | | Stage-class at year $t$ | | | |
| **Projection matrix** | | | | ($\lambda=1.0286$) | | | |
| S | 0 | 0 | 0 | 0 | 0 | 0 | 5.94 |
| $J_1$-I | 0.601 | **0.730** | 0.204 | 0 | 0 | 0 | 0 |
| $J_2$-I | 0.0119 | 0.0321 | **0.612** | 0 | 0 | 0 | 0 |
| $J_1$-II | 0 | 0.0232 | 0 | **0.778** | 0 | 0 | 0 |
| $J_2$-II | 0 | 0 | 0.0204 | 0.160 | **0.906** | 0 | 0 |
| $J_2$-III | 0 | 0 | 0 | 0 | 0.0591 | **0.970** | 0 |
| M | 0 | 0 | 0 | 0 | 0 | 0.0182 | **0.998** |
| SR | 0.613 | 0.786 | 0.837 | 0.938 | 0.966 | 0.988 | 0.998 |
| **Elasticity matrix** | | | | | | | |
| S | 0 | 0 | 0 | 0 | 0 | 0 | 0.0148 |
| $J_1$-I | **0.0144** | **0.0375** | 0.000949 | 0 | 0 | 0 | 0 |
| $J_2$-I | 0.000379 | 0.00220 | **0.00380** | 0 | 0 | 0 | 0 |
| $J_1$-II | 0 | 0.0131 | 0 | **0.0407** | 0 | 0 | 0 |
| $J_2$-II | 0 | 0 | 0.00163 | 0.0131 | **0.110** | 0 | 0 |
| $J_2$-III | 0 | 0 | 0 | 0 | 0.0148 | **0.243** | 0 |
| M | 0 | 0 | 0 | 0 | 0 | 0.0148 | **0.475** |
| Σ | 0.0148 | 0.0529 | 0.00638 | 0.0538 | 0.124 | 0.258 | **0.490** |

SR=survival rate for each stage-class. Population growth rate ($\lambda$) is shown. Total number of available data for calculating transition probabilities=1347. Bold letters in the projection and elasticity matrices show the diagonal elements and the highest values of each column, respectively.

dence concerning demographic parameters and population dynamics of this typical riparian species. The evidence shows the effects of environmental constraints on different growth stages of individuals in different subpopulations, showing that the levels of constraints are different among the three subpopulations in response to differences in the disturbance regimes and in competition.

### Changes in the demographic parameters of subpopulations and environmental constraints in riparian habitats

*Matrix and elasticity analyses, and their implications.* The circumstances of population dynamics in *Aesculus* in the valley system are more unequivocally shown in the matrix analyses for the whole population which consisted of three subpopulations developed at the different topographic habitats. The elasticity analysis for the whole population showed the relative importance of the slope subpopulation, suggesting its significant roles as the main source of offspring recruitment over an environmental gradient and as main subpopulation supporting the whole population (Table 6b). A question arising here is why, in spite of the fact that *Aesculus* is predominant

there, the elasticity values are so low in the terrace subpopulation. Are there any specific underlying factors that cause elasticity to be very low?

If we compare the survival rates of S, $J_1$-I, and $J_2$-I stages between the slope and terrace subpopulations, the latter subpopulation shows much lower rates for the early juvenile growth stage from seedlings, monopodial juveniles, and branching juveniles lower than 1 m in height (Fig. 13; Table 6a), reflecting strong competitive interactions, primarily due to strong shading effects, between the dwarf bamboo, *Sasa senanensis*, and young juveniles of *Aesculus*. At these growth stages (S, $J_1$-I, and $J_2$-I), individuals which are below the bamboo thickets often return to the lower growth stages from $J_2$-I to $J_1$-I or stay in the same stage (Table 6a), while individuals which grow in gaps are likely to proceed to the next growth stages. This situation is in part mirrored in the maximum growth rates of $J_2$-II and $J_2$-III (Fig. 11). However, generally speaking, individuals in the juvenile stages exhibit much faster growth once they overtop the bamboo and other shrub layers approximately 4 m in height, showing even higher growth rates than those of the slope subpopulation (Table 6a). All this available evidence indicates that the exceedingly low elasticity values of the terrace juveniles, notably those at the S, $J_1$-I, and $J_2$-I stages, are due to this sup-

**Table 6** The (a) projection and (b) elasticity matrix for the whole population consisting of three subpopulations developed at the different topographic habitats: slope, terrace, and floodplain

### (a) The projection matrix

$(\lambda = 1.0298)$

| Stage-class at year $t+1$ | Slope (S) S | J₁-I | J₂-I | J₁-II | J₂-II | J₂-III | M | Terrace (T) S | J₁-I | J₂-I | J₁-II | J₂-II | J₂-III | M | Floodplain (F) S | J₁-I | J₂-I | J₁-II | J₂-II | J₂-III |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **S** S | 0 | 0 | 0 | 0 | 0 | 0 | 3.68 | 0 | 0 | 0 | 0 | 0 | 0 | 5.14 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-I | 0.783 | **0.771** | 0.167 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-I | 0 | 0.0246 | **0.750** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-II | 0 | 0.0387 | 0 | **0.828** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-II | 0 | 0 | 0 | 0.121 | **0.917** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-III | 0 | 0 | 0 | 0 | 0.0661 | **0.981** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M | 0 | 0 | 0 | 0 | 0 | 0.00952 | **0.996** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **T** S | 0 | 0 | 0 | 0 | 0 | 0 | 0.827 | 0.308 | 0 | 0 | 0 | 0 | 0 | 1.16 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0256 | **0.739** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0332 | 0.400 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.00474 | **0.300** | **0.769** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.100 | 0.154 | **0.909** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-III | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0545 | **0.963** | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0370 | **0.997** | 0 | 0 | 0 | 0 | 0 | 0 |
| **F** S | 0 | 0 | 0 | 0 | 0 | 0 | 0.663 | 0 | 0 | 0 | 0 | 0 | 0 | 0.928 | 0.459 | **0.523** | 0.133 | 0 | 0 | 0 |
| J₁-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0270 | 0.0615 | **0.600** | **0.500** | 0 | 0 |
| J₂-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0154 | 0 | **0.400** | 0 | 0 |
| J₁-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **0.852** | 0 |
| J₂-III | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0370 | **0.841** |
| **SR** | 0.783 | 0.835 | 0.917 | 0.948 | 0.983 | 0.990 | 0.996 | 0.333 | 0.777 | 0.800 | 0.923 | 0.964 | 1.000 | 0.997 | 0.486 | 0.600 | 0.733 | 0.900 | 0.889 | 0.841 |

### (b) The elasticity matrix

| Stage-class at year $t+1$ | Slope (S) S | J₁-I | J₂-I | J₁-II | J₂-II | J₂-III | M | Terrace (T) S | J₁-I | J₂-I | J₁-II | J₂-II | J₂-III | M | Floodplain (F) S | J₁-I | J₂-I | J₁-II | J₂-II | J₂-III |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **S** S | 0 | 0 | 0 | 0 | 0 | 0 | 0.0114 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-I | **0.0127** | **0.0402** | 0.000765 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-I | 0 | 0.000765 | **0.00205** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-II | 0 | 0.0127 | 0 | **0.0521** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-II | 0 | 0 | 0 | 0.0127 | **0.104** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-III | 0 | 0 | 0 | 0 | 0.0127 | **0.256** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M | 0 | 0 | 0 | 0 | 0 | 0.0127 | **0.375** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **T** S | 0 | 0 | 0 | 0 | 0 | 0 | 0.00134 | **0.00102** | 0 | 0 | 0 | 0 | 0 | 0.00134 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.000480 | **0.00290** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.000736 | 0.000118 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.000405 | 0.000500 | **0.00120** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **0.00110** | 0.000405 | **0.0113** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-III | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.00150 | **0.0217** | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| M | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.00150 | **0.0464** | 0 | 0 | 0 | 0 | 0 | 0 |
| **F** S | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.000159 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₁-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-II | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| J₂-III | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Σ** | 0.0127 | 0.0537 | 0.00281 | 0.0649 | 0.117 | 0.269 | 0.388 | 0.00150 | 0.00405 | 0.00172 | 0.00160 | 0.0128 | 0.0232 | 0.0479 | 0 | 0 | 0 | 0 | 0 | 0 |

SR=survival rate for each stage-class. Total number of available data for calculating transition probabilities is 1347. Bold letters in each submatrix show (a) the diagonal elements and (b) the highest values of each column.

**Fig. 14** Relationships between gap-size and the (a) stage-class (□, $J_1$–I; ▨, $J_2$–I; ◨, $J_1$–II; ▤, $J_2$–II; ■, $J_2$–III) and (b) age-class (□, 1–5; ▨, 6–10; ▥, 11–15; ▨, 16–20; ▦, 21–25; ▨, 26–30; ■, 31–) compositions in 1992. *S, gap whose cause was on the slope site; T, gap whose cause was on the terrace sites. **5, mode of age distribution in 5-year age-class; 5, 16, mode of age distribution in 5- and 16-year age-classes; 3, 16, mode of age distribution in 3- and 16-year age-classes. Gap numbers correspond to the numbers in Fig. 3. Gap area (m²): gap no. 1 = 373.1, 2 = 204.2, 3 = 173.6, 4 = 132.1, 5 = 72.5, 6 = 46.7.

pressed condition at the young growth stages, but further implications of these low elasticity values need to be more critically examined by simulation study.

Considering the recruitment processes, the significance of the slope environment is very evident, and the differences between the slope and other adjacent sites supported the present frequency distribution patterns of abundance of newly recruited seedlings (Table 6a; Fig. 7). This difference is obviously caused by the light and soil

conditions of the slope sites, where are better for survival of seeds and current-year seedlings. In the other sites, environmental stresses and physiological disorders due to pathogen attacks were also the main mortality factors.

In summary, the results of elasticity analysis for the whole population which consisted of three subpopulations developed at the different topographic habitats indicate that a slope subpopulation has a higher potential than a terrace subpopulation for maintenance of the whole population in riparian habitats. The densities of *Aesculus* populations in three different habitats clearly reflected the differences in their environmental constraints, not only the disturbance regimes of each habitat but also biotic interactions between or among the major community components, and interactions in the shrub and dwarf bamboo layers (Table 1).

In riparian environments under complex disturbance regimes, tree population dynamics are considered to be dependent on changes in demographic parameters caused by environmental factors, especially after occasional disturbances. Therefore, transition models with temporarily constant elements are only indicators of current demographic trends. Simulations using transition models incorporating the effects of disturbance regimes would be useful as projections of long-term population behaviors.

*Implications of vital rates.* Differences in the vital rates were also examined for individuals at different growth stages in the three subpopulations. The differences in demographic features of the three subpopulations are evident, reflecting the critical phases of recruitment: stability of substratum, establishment rates of seedlings, and growth and mortality and/or vitality of prereproductive juveniles ($J_2$-III). The prereproductive juveniles are obviously at a disadvantage in the floodplain, judging from the higher mortality rate and lower growth rate. This difference was perhaps caused by the differences between the regeneration mechanisms of terrace and floodplain subpopulations.

The significance of a slope subpopulation in the recruitment process is evident when its demographic parameters are compared with those of the two other subpopulations. The census data (Fig. 6) show that *Aesculus* is more than twice as abundant on the slope as on the terrace. This species is also predominant in the terrace, along with *Acer nipponicum* and *Quercus mongolica* var. *grosseserrata* and the dwarf bamboo layer, although the total density is much lower than that on the slope. The density of mature trees is more or less at the same level in both the terrace and slope sites, but mean d.b.h. and ages of mature trees are greater in the terrace than on the slope. The calculated survival rates of individual trees

above 30 cm in d.b.h. of all tree species, including both the canopy and subcanopy layers, show that those of the terrace (98.4%) are slightly higher than those of the slope (97.3%), just as seen in *Aesculus* (Table 6a), but lowest in the floodplain (97.1%).

## Seed dispersal within and among subpopulations

Another important question is: what are the patterns of population dynamics found in *Aesculus* over the environmental gradient in the riparian habitats? Are there any significant dispersal agents for establishment of offspring populations for each subpopulation?

Plants are essentially sedentary, but they migrate as propagules to the surrounding sites in their habitats; extremely long-distance dispersals via wind, sea currents, or migratory birds are also well known in many plants (van der Pijl 1969). Clonal plants also shift their positions by new offshoot formation and root sucker elongation, often by several meters or more per year, and expand their patches rapidly (de Kroon & van Groenendael 1997).

Seed dispersal of *Aesculus* depends upon a combination of barochory and synzoochore (by wood mice) (Miguchi 1994, 1996). According to our seed-trap data, seed recruitment on the floodplain was by barochory, from mature trees on the slope and terrace sites (Table 2). Subpopulations in floodplain sites are thus considered to be sink populations, which will disappear if there is no continuous seed flow from other neighboring sites (Table 6a). The floodplain subpopulation is therefore highly dependent on seed supply from the surrounding sites.

Some seeds were predated by mammals around the point where they fell before secondary dispersal, and almost all seeds that fell to the ground were dispersed secondarily by wood mice. Almost all cotyledons remaining in the soil layer were again transported by wood mice after germination, sometimes with damage to aerial shoots (epicotyls), occasionally with stem-cutting (Y. Kaneko, unpubl. data, 1991–1993). However, synzoochore (by wood mice) is considered to contribute to seed dispersal of the Japanese horse chestnut from the terrace to the safe sites on the slope. Wood mice (mainly *Apodemus speciosus*) are also known to carry seeds selectively into the sites in a gap rather than those under the closed canopy sites (Miguchi 1994, 1996).

Therefore, they may be playing an important role in the population dynamics of *Aesculus*. The entire *Aesculus* population spread over three different sites (from slope to terrace or terrace to floodplain) is, thus, linked and maintained by these two mechanisms of seed dispersal.

In light of the actual seed trap data (Table 2; Fig. 7), we can see the efficiency and potential importance of each subpopulation for population maintenance. Seed supplies

from slope and terrace subpopulations clearly show differences: the rates of seed supply from the slope subpopulation are 0.65 within the slope, 0.14 to the terrace, and 0.21 to the floodplain; those from the terrace subpopulation are 0.29 within the terrace, the major portion, 0.71, to the floodplain, and probably some to the slope (possibly dispersed by wood mice), although no exact data are available at present.

## The roles of gaps for recruitment and maintenance of Aesculus *populations in different riparian habitats*

In riparian habitats, new gaps of various sizes are often created by landslides or treefalls, or after synchronized flowering of *Sasa kurilensis* or *S. senanensis*, typical monocarpic dwarf bamboos and predominant elements in mixed forests in northern to central Japan. The riparian habitats are also often exposed to occasional disturbances such as flooding caused by typhoons or storms, which creates numerous gaps of various sizes with variable substratum conditions.

Gaps on the slope are obviously safe sites for seeds and current-year seedlings, and gaps on the terrace with thick and resource-abundant forest soil also provide suitable environments for the establishment of seeds and current-year seedlings of *Aesculus* (Fig. 14).

On the floodplain, a few but large gaps, which often are quite destructive, are occasionally formed by two or more gap makers (Runkle 1990), and thus the percentages of the total gap areas to total study area are highest there (Table 1 and Yamanaka *et al.* 1997). However, these canopy gaps formed by a physically destructive event such as a typhoon are usually accompanied by geomorphic disturbances, which often entirely alter the forest floor and create numerous new gaps and these gaps are not always safe sites for *Aesculus*. In these new open sites, overly moist immature soil often prevents germination of dispersed seeds from terrace and slope, and inhibits growth of the main roots of current-year seedlings of *Aesculus*.

In contrast, on the slope many small gaps (empty patches) are often formed by a single or a few gap makers, although the proportions of total gap areas on slopes are lowest of all the environments (Table 1). These canopy gaps created by small-scale treefalls or branchfalls are not usually accompanied by geomorphic disturbances of the forest floor and are safe sites for seeds and current-year seedlings of *Aesculus*, because a thicker and more mature forest soil develops, even though large-scale geomorphic disturbances due to landslide sometimes occur. A terrace has no geomorphic disturbance agent of its own and thus is a quite stable habitat, although the effects of a large-scale landslide on the slope or flooding in the river can occasionally reach the terrace, and gaps are created there

too. Likewise, gaps are formed on the forest floor of the terrace after synchronized flowering of monocarpic *S. kurilensis* or *S. senanensis*. As above, terrace gaps are suitable for *Aesculus*.

It is now evident that an exceedingly large number of small, medium, and large gaps are formed along the Mondoridani river system (Fig. 3). The relationships between the size of gap areas and the density of *Aesculus* plants belonging to different stage- or age-classes distinguished based upon the positions and numbers of leaf bud scars are shown in Fig. 14. It is apparent that the larger the gap areas are, the more proportionately predominant are individuals of younger and earlier growth stages within gap populations.

In smaller gaps in terrace and slope environments, older individuals and/or advanced stage-classes were more abundant, suggesting that smaller gaps are older. Individuals on the floodplain primarily survive under the canopy, but their numbers dramatically decrease due to shading and frequent disturbances of the habitats; those on the terrace survive in the canopy gaps where light and soil conditions are favorable (Figs 3 and 14). In short, the three subpopulations have different patterns of vital rates at the two developmental stages: the seedling and prereproductive juvenile phases.

### Population dynamics of Aesculus *in view of the metapopulation concept and its implications for demographic analyses*

We need to mention here the spatiotemporal changes of *Aesculus* populations in light of the metapopulation concept (Hanski & Gilpin 1997). An understanding of the interaction of demographic and genetic factors in plant populations provides us a new focus for fundamental advances at the interface of ecology and evolution (Lande 1988; Olivieri *et al*. 1990; Eriksson 1996). In the classic metapopulation concept (Levins 1969), metapopulation is defined as a large network of small population patches of similar sizes with local dynamics of colonizations and extinctions occurring at relatively short time intervals (Hanski & Simberloff 1997). Recent theoretical (Hanski 1996; Husband & Barrett 1996; Hedric & Gilpin 1997) and empiric works (Alvarez–Buylla *et al*. 1996; Giles & Goudet 1997; Kawano & Kitamura 1997; Kitamura *et al*. 1997a,b) have shown the implications of the metapopulation concept in studies of population dynamics and demographic genetic differentiations in plant populations.
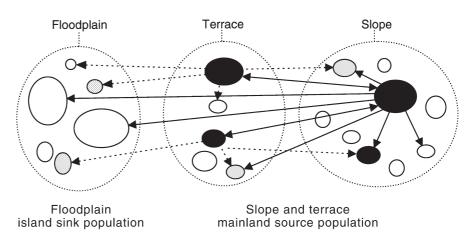
In general, plant populations consist of various scales of patchy distributions in biotic communities or natural landscapes. We can recognize a hierarchical substructuring of populations in varying levels of patchiness. We have called the smallest assemblage of individuals in a habitat a patch or a patch population (Young *et al*. 1993;

Young & Merriam 1994; Kawano & Kitamura 1997; cf. also Kudoh *et al*. 1999). A group of adjacent patch populations which are linked by a significant gene flow constitute a local population. And these local populations within a larger area constitute a metapopulation, a more loosely structured assemblage of local populations and empty patch habitats which are more or less linked by gene flow through pollen and/or seed dispersal. However, in woody species which have much longer life spans, often exceeding several hundred years, fragmentation and fusion of patch populations, as well as emergence of various sizes of gaps (empty patches) within a habitat, may proceed gradually, especially under natural conditions. The size and number of established patch populations within a local population are quite variable, and as a consequence, the range of gene flow within and between and/or among patch populations may be restricted or expanded. Young and Merriam (1994) examined the effects of forest fragmentation on the spatial genetic structure of sugar maple populations, and demonstrated that mating events are the primary determinant of spatial genetic structure within cohorts in both patch and mainland populations. Forest fragmentation has affected genetic structure by changing patterns of gene flow within, and possibly among, forest patch populations. A somewhat similar situation was lately discovered in the fragmented and isolated Japanese beech populations in the lowlands of the Hokuriku district, Honshu, where $G_{ST}$ values of these fragmented populations in the lowlands are highly elevated, as compared with the large mainland populations developed on the montane zone (Ohkawa *et al*. 1999).

We have consistently in the present paper called a local unit of *Aesculus* populations a subpopulation, since without detailed data concerning the range and extent of pollen flow (the degree of gene exchange) and seed dispersal within the whole population of the study area, we cannot strictly apply such population categories as patch or patch population, local population, etc., as defined above. Recent evidence on the gene flow among *Aesculus* individuals in the Mondoridani study site by means of DNA microsatellite markers suggests that the range of pollen flow is much broader in this insect-pollinated woody species (Minami *et al*. 1998; Y. Isagi *et al*. unpubl. data, 1997–1999). *Aesculus* is known to be pollinated by large bumble bees, *Bombus hypocrita* and *Bombus ardens* (Kakutani 1994), which obviously forage over a broad territory.

Figures 5 and 15 demonstrate diagrammatically the efficiencies of recruitment, directions of seed dispersal, and life-history processes of *Aesculus* within each subpopulation and the relationships between currently existing adjacent subpopulations and various sizes of possible empty patches. In changing environments like river

**Fig. 15** Diagram summarizing and illustrating metapopulation structure for *Aesculus*. In light of the metapopulation concept (Hanski & Gilpin 1997), *Aesculus* population could be regarded as a mainland-island type of metapopulation in the sense of Harrison and Taylor (1997). The slope and terrace subpopulation together could be regarded as a mainland source population, while a floodplain subpopulation cannot persist without seed supplies from terrace and/or slope subpopulations, and thus resembles a typical island sink population. ●, occupied habitat patches (= patch populations) with mature trees; ⊙, occupied habitat patches (= patch populations) with no mature trees; ○, empty habitat patches (= gaps in case of a forest); ····, boundaries of local populations (= subpopulations); arrows, seed dispersal (= a significant gene flow).

floodplains, frequent changes occur in the size of favorable sites (e.g. gaps or empty patches) for a particular species, and such changes might cause occasional fragmentations and reunions of the patch populations. Simultaneously, open empty patches will be available for many other species, and thus there will be an increasing competitive interaction among various pioneers at the early small-scale successional processes. Sudden extreme disturbances may also eliminate some patches or subpopulations, and a stronger isolation between/among these local units of individual assemblages may arise due to disappearance and fragmentation.

Dynamic changes of various degrees are unique in the floodplain habitats developed along the stream of the valley system. The circumstances here revealed in *Aesculus* populations could be referred to as a mainland-island state in the sense of Harrison and Taylor (1997). In short, the slope and terrace subpopulation together could be regarded as a mainland source population, while a floodplain subpopulation cannot persist without seed supplies from terrace and/or slope subpopulations, and thus resembles a typical island sink population. The slope and terrace subpopulations developed on the more or less continuous extension of an environmental gradient over a riparian habitat obviously share a complementary role in maintaining *Aesculus* populations in the changing environments of the riparian zone. As summarized and illustrated in Fig. 15, the main sources of seed supplies in an *Aesculus* metapopulation are obviously from the slope subpopulation. Due to the instability of floodplain habitats, the rates of seed establishment there are very low, despite the fact that there occur numerous empty patches ('gaps'). We have to question here the roles of floodplain subpopulation for the maintenance of the *Aesculus* population in the riparian habitats (i.e. whether or not it has a

simply temporary patch population at the marginal habitat).

However, there is another counterpart species known as a typical riparian element, *Pterocarya rhoifolia* in the Mondoridani valley; without knowing exactly the behaviors of this sister riparian species, we cannot illustrate the total picture of population dynamics and demographic characteristics of *Aesculus* itself, and such an attempt is now being also made (Y. Kaneko *et al.*, unpubl. obs., 1989–1999).

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