Ann. For. Sci. 64 (2007) 405–412
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DOI: 10.1051/forest:2007017

Available online at:
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**Original article**

# Steep slopes promote downhill dispersal of *Quercus crispula* seeds and weaken the fine-scale genetic structure of seedling populations

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(Received 26 June 2006; accepted 19 January 2007)

**Abstract –** The seed dispersal patterns and genetic structure of plant populations in mountainous forests may differ from those on flat sites, because some seeds that fall from adults are likely to roll downhill, and thus cause the seed shadows from different mother trees to merge. In the study reported here we used six polymorphic microsatellite markers to track seed dispersal and examine the fine-scale spatial genetic structure of adults and first-year seedlings of *Quercus crispula* in 2500 $m^2$ plots on four slopes. In each of the four plots, leaves of adults, seedlings and endocarps of hypogeal cotyledons attached to the seedlings were genotyped to identify the seedlings' mother trees. The results showed that steeper slopes result in larger dispersions and smaller genetic structure of seedlings. These findings are a crucial step towards an understanding of the effect of topography on tree regeneration.

**genetic structure / microsatellite marker / *Quercus crispula* / seed dispersal / slope**

**Résumé – Influence des pentes fortes sur la dispersion et la structure génétique des populations de *Quercus crispula*.** Les modes de dispersion des graines et la structure génétique des populations d'arbres peuvent être différents en forêts de montagne par rapport à ceux en forêts de plaine. En effet, les graines qui tombent des arbres adultes roulent probablement vers le bas de la pente entraînant un regroupement des descendances de différentes mères. Dans cette étude, nous avons suivi la dispersion des graines de *Quercus crispula* et nous avons examiné à l'aide de six marqueurs microsatellites polymorphiques la structure spatiale génétique des arbres adultes et de leurs descendants (semis de 1 an) sur des placeaux de 2500 $m^2$ dans quatre pentes. Dans chacun des placeaux, les feuilles des arbres adultes et des semis ainsi que les endocarpes des cotylédons attachés aux semis ont été génotypés de manière à identifier les mères des semis. Les résultats montrent que les pentes fortes contribuent à une forte dispersion et à une faible structuration génétique des semis. Ces résultats sont une étape importante pour la compréhension des effets de la topographie sur la régénération des arbres.

**structure génétique / marqueur microsatellite / *Quercus crispula* / dispersion des graines / pente**

## 1. INTRODUCTION

Information on seed dispersal and genetic structure is very important for elucidating the processes involved in the establishment of forests and for forecasting future changes in their composition and dynamics. Many studies of seed dispersal have concentrated on long-distance dispersal, since it influences many key aspects of plant biology, including the spread of invasive species, metapopulation dynamics, and the diversity of plant communities [3, 28, 32]. Similarly, most previous studies of genetic variation within plant populations have focused on variation at the macrogeographic ($10^2 \sim 10^3$ km) scale [1, 5, 21, 24]. Information on seed dispersal and microgeographic or fine-scale genetic structure, on the other hand, is also important for elucidating fine-scale evolutionary processes such as the establishment of sibling neighborhoods and fine-scale selection effects [6]. However, several recent studies have inferred general patterns in populations where limited gene flow has resulted in fine-scale genetic structure, with 'patches' of genetically similar individuals [2, 6, 14, 33], in accordance with the neighborhoods or demes theoretically proposed by Wright [37].

However, seed dispersal patterns and the genetic structure of populations in mountainous forests may differ from those on flat sites and those proposed by Wright [37] because some seeds that fall from adults are likely to roll downhill, causing the seed shadows of different mother trees to overlap. Shiokawa and Kagaya [26] have reported that litter from deciduous trees on slopes of around 30° in Japan moves downhill at a rate of 1200 g/m/y. Similarly, seeds which are dispersed by gravity may also move downhill, thereby limiting the formation of fine-scale genetic structure. Such processes may occur widely, because many forests are located in mountainous regions. However, few researchers have previously examined

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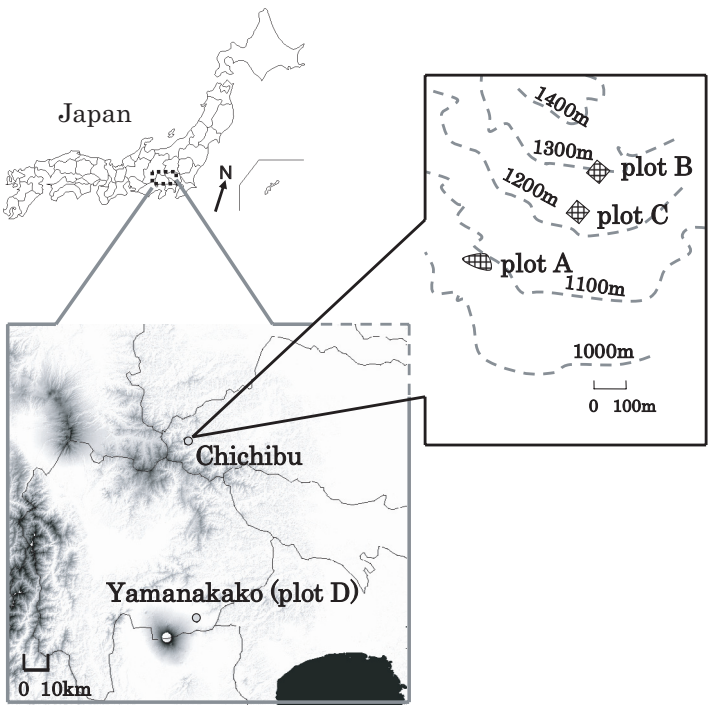


**Figure 1.** Location of the three *Q. crispula* plots in the University Forest in Chichibu and the single plot in the University Forest in Yamanakako. This map of the central Japan was prepared by use of the software Kashmir 3D, by Tomohiko Sugimoto.

whether such processes actually occur in mountains or not, although fine-scale genetic structure due to limited gene flow at flat sites has been extensively investigated. This is partly because no convenient methods for monitoring seed dispersal have been available until fairly recently [3, 22, 35]. For example, Sork [29] examined seed dispersal of *Quercus rubra* using metal tags, but such methods are time- and labor-intensive in the field. Furthermore, many tags may be missed. However, recent advances, such as the development of stable isotope ratio and molecular genetic marker techniques, are helping to overcome this difficulty [12, 35]. For example, Grivet et al. [10] successfully tracked seeds dispersal by acorn woodpeckers (*Melanerpes formicivorus*) in granaries using microsatellite markers.

*Quercus crispula* Blume (Fagaceae) is a common tree species throughout the cool temperate deciduous forests of southern Sakhalin, the Kuril Islands, Japan and Korea. It is intermediately shade-tolerant, capable of sustained regeneration, and lives for several hundred years, attaining a maximum height and diameter of 30 m and 1.5 m, respectively [36]. *Q. crispula* is a monoecious, highly out-crossed, and wind-pollinated species [36]. Its seeds are dispersed by gravity or rodents and birds, and supply important foods for animals [36]. Thus it is an important species in the forest ecosystem, and is also economically valuable for forestry. Since its large (length: 2−3 cm, width: 1.2−1.5 cm) [11] and heavy (fresh weight: 1.7−4.3 g) [25] seeds are likely to roll downhill, this species is suitable for elucidating the effects of slope on seed dispersal and fine-scale genetic structure.

In the study reported here we tracked seed dispersal and examined the genetic structure of *Q. crispula* populations on various slopes using polymorphic microsatellite markers. Few seeds survive to become seedlings, and few seedlings reach the adult stage. So, information on seedlings is more valuable than information on seeds for assessing the effects of slopes on forest establishment. For this reason we focused on seed dispersal and genetic structure at the seedling stage. More specifically, the following questions were addressed. First, in which direction and to what extent are seeds of *Q. crispula* dispersed on slopes? Second, is genetic structure formed even on slopes? And if so, it is weaker than on flat sites?

## 2. MATERIALS AND METHODS

### 2.1. Field Site and Sampling

This study was performed in the University of Tokyo Forests in Chichibu (138° 48' E, 35° 56' N) and Yamanakako (138° 52' E, 35° 24' N), both of which are located in the central area of Japan (Fig. 1). The major oak species in this region are *Q. crispula* and *Q. serrata,* the latter predominantly in warmer areas than *Q. crispula*. Two study plots (plots A and B) were established in 2004 and one plot (plot C) in 2005 on the same southwest-facing hillside in this forest. The meteorological data, which were recorded at near to the southwest-facing hillside from 2001 to 2004, indicate that the strong wind, whose maximum velocity was larger than 10 m/s, has generally blown from west in 0 to 3 days per month in autumn [34]. Probably this is caused by typhoon. The adult trees in the sampling

plots were around 70 years old. One plot (plot A) consists of a fragmented forest composed of 35 mature oak trees (33 *Q. crispula* and 2 *Q. serrata*), in a triangular area of 2500 $m^2$, situated on a steep slope (around 31°). Such steep areas with poor soil escaped afforestation, although the surrounding forests have been replaced by artificial forests of conifers. The nearest natural forest to this stand is 50 m away. By contrast, plot B covers an area of 50 m × 50 m plot on a gentle slope (around 19°), in which there were 72 adults of *Q. crispula*. Similarly, plot C covers an area of 50 m × 50 m on a gentler slope (around 9°), in which there were 35 adults of *Q. crispula*. The vegetation at the three plots is similar – consisting of secondary deciduous forests dominated by *Q. crispula*, *Fagus crenata*, and *Acer* spp. Seed-dispersing animals, including mouse (*Apodemus speciosus* and *Apodemus argenteus*), squirrel (*Sciurus lis*), jay (*Garrulus glandarius*), spotted nutcracker (*Nucifraga caryocatactes*) and varied tit (*Parus varius*) have been identified in the Chichibu Mountains [13]. In addition, one 50 m × 50 m plot (plot D) was established in 2005 on a flat site (around 6°) in the University Forest in Yamanakako as a reference. In this plot, there were 12 adults of *Q. crispula*.

We collected leaves of every adult and all seedlings that germinated in 2004 in plots A and B, and in 2005 in plots C and D, to detect and compare vertical dispersal events on steep and gentle slopes. The endocarps of hypogeal cotyledons attached to the seedlings were also sampled, where possible, since the endocarp is a tissue of maternal origin, allowing the mother trees of the respective seedlings to be identified [9, 10, 31]. However, too many seedlings germinated in 2005 in plot C to analyze them all, so we collected at random one fifth of these seedlings, together with their endocarps. The collected samples were stored at −80 °C until DNA extraction. The location of individuals found within each plot was also recorded.

## 2.2. Genetic analysis

DNA was extracted by a modified CTAB procedure [38]. However, the sampled endocarps had been buried under ground for more than six months, and the sampled material included impurities. Therefore, polymerase chain reaction (PCR) amplification of the endocarp DNA was often imperfect or resulted in multiple bands that were difficult to genotype. In an attempt to solve these problems, the endocarp extracts were purified using a Wizard SV Gel and PCR Clean-Up System (Promega) before PCR amplification using a multiplex PCR Kit (QIAGEN) with six nuclear microsatellite (SSR) primers: QpZAG1/5, QpZAG9, QpZAG15, QpZAG16, QpZAG110 [30] and MSQ13 [8]. Maternally inherited chloroplast DNA markers were not used because of a lack of variation at the scale of this study. The 5.0 μL amplification reaction mixtures included 2.5 μL of MasterMix solution (QIAGEN), 1.3 μL of RNase-free water, 0.5 μL of primer mix solution, and 0.7 μL of extracted DNA solution (10−100 μg/mL for leaf DNA and 10−50 μg/mL for endocarp DNA). The primer mix solution included six primer pairs, each at a concentration 0.5 pmol/μL. The reactions were performed with the following temperature program: 15 min denaturing at 95 °C followed by 30 cycles of 30 s denaturing at 94 °C, 90 s annealing at 57 °C and 60 s extension at 72 °C, with a final extension step of 60 °C for 30 min. For the endocarp DNA, the number of PCR cycles was increased from 30 to 40, to ensure sufficient amplification for genotyping. Finally, the PCR products were loaded into an ABI3100 Genetic Analyzer (Applied Biosystems) and amplified allele sizes were determined using GeneMapper software (Applied Biosystems).

## 2.3. Parentage analysis

We determined the genotypes of all the sampled adults and seedlings with respect to all six of the markers, but the endocarps were genotyped with respect to only three markers (QpZAG1/5, QpZAG16, and MSQ13) in order to avoid miss-genotyping them. After the genotyping we calculated the Polymorphism Information Content (PIC) of each marker using the CERVUS program [19] to estimate their resolution power. In CERVUS, PIC is defined as following formula:

$$\mathrm{PIC} = 1 - \left(\sum_{i=1}^{n} p_i^2\right) - \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} 2 p_i^2 p_j^2$$

where $p_i$ and $p_j$ are the frequencies of the $i$th and $j$th alleles in the population. To identify the mother trees of the seedlings in the four plots, we then detected adult trees with genotypes that exactly matched those of endocarps at the three markers, regarding such adults as the mothers of the respective seedlings. In cases where more than one tree genotypically matched an endocarp, the other three markers were also used to identify the true mother tree. However, few endocarps from plot A were successfully genotyped. Therefore, we identified the mother tree of seedlings whose endocarp had not been found or genotyped in plot A, by recording the genotypes of adults and the seedlings at six markers. Before this parentage analysis, we calculated the total exclusion probability (EP) [4] for the first parent in plot A using the CERVUS program in order to estimate the resolution power of these six markers. The exclusion probability $\mathrm{EP}_l$ at a locus $l$ with $k$ codominant alleles is given by:

$$\mathrm{EP}_l = a_1 - 2a_2 + a_3 + 3\left(a_2 a_3 - a_5\right) - 2\left(a_2^2 - a_4\right)$$

where $a_n = \sum_{i=1i}^{k} p_i^n$ And $p_i$ is the frequency of allele $i$, and $a_1 = 1$ [4]. If then $M$ loci are investigated, $EP$ is:

$$\mathrm{EP} = 1 - \prod_{l=1}^{M} (1 - EP_l)$$

We then conducted a simple parentage exclusion analysis by the following procedure. If a seedling matched no adult in the forest, its parent trees were assumed to be located outside of the sampled plot. Second, if a seedling matched only one adult in the plot, the matching adult was assumed to be its maternal rather than paternal parent, because of the low assumed probability of a female flower located outside the plot being fertilized by pollen from within the plot and developing a seed that is subsequently transported into the plot. Similar approaches have been applied in previous studies [7]. Third, if a seedling matched multiple adults in the forest, both of its parent trees were assumed to be present in this forest, but its mother tree could not be identified from the multiple candidates.

## 2.4. Seed dispersal analysis and supplementary survey

We calculated the spatial vectors ($x$, $y$, $z$) of seed dispersal based on the positions of seedlings and their respective mother trees. The direction of the horizontal ($x$ and $y$) axes have no particular significance, while the positive and negative orientations along the $z$ axis indicate up and down from the base of the maternal tree, respectively. The mean horizontal and vertical dispersal distances were then

**Table I.** Field site characteristics and description of the *Q. crispula* sampled.

| | Plot A | Plot B | Plot C | Plot D |
|---|---|---|---|---|
| Location | Chichibu | Chichibu | Chichibu | Yamanakako |
| Altitude | 1100m | 1300m | 1200m | 1000m |
| Study year | 2004 | 2004 | 2005 | 2005 |
| Mean gradient | 31° | 19° | 9° | 6° |
| Number | | | | |
| Adults | 35 | 72 | 35 | 12 |
| Collected seedlings | 70 | 238 | 232* | 126 |
| Collected endocarps | 52 | 216 | 125 | 120 |
| Genotyped endocarps | 36 | 172 | 116 | 104 |
| Seedlings whose mother trees were identified | 62** | 111 | 79 | 83 |

* 1160 seedlings were found in plot C, but only 232 of them were randomly selected.
** Mother trees of seedlings whose endocarps were not genotyped in plot A were identified following the approach of Dow and Ashley [7].

calculated from the resulting vectors. To compare the dispersal distance distributions among plots, histograms were described. Upward dispersal was distinguished from other dispersal events. To discriminate between upward dispersal mediated by animals and gravity, we mapped the seed dispersal and crown projection of every mother tree for which daughter seedling had been identified above the point at which it was rooted. Seeds may fall from the crown of a mother tree to sites above the point at which it is rooted. Thus, short upward dispersal within the mother tree's crown projection is probably caused by gravity. However, the seeds of *Q. crispula* are heavy and wind generally has little effect on their dispersal. So, upward dispersal beyond the mother tree's crown projection is probably caused by animals. In this study, the seeds that had settled within the upper portion of their mothers' crowns were assumed to have been dispersed by gravity, while those that had settled above and beyond their mother trees' crowns were assumed to have been dispersed by animals.

### 2.5. Fine-scale genetic structure

Spatial genetic structure was assessed using a spatial autocorrelation approach for multilocus genotypes based on genetic distance methods. For this purpose the distances between the seedlings and adults in all four plots were classified in 5-m intervals, and the GenAlEx 5.1 program [23] was used to calculate the spatial autocorrelation coefficient ($r$) [27]. Briefly, Smouse and Peakall [27] defined the genetic distance, $d_{ij}$, between a pair of individuals, considering a trio of codominant alleles ($A, B, C$) and a sextet of diploid genotypes. In the triangle consisted of the three vertexes, $d_{ij}$ between heterozygotes sharing a single allele (ex: $AB$ and $AC$) is 1, and that between any heterozygote and the opposite vertex homozygote (ex: $AB$ to $CC$) is $\sqrt{3}$. Again, $d_{ij}$ between any genotype and itself is 0. To obtain a multilocus distance, Smouse and Peakall [27] simply add the squared values of $d_{ij}$ across loci. The multilocus distance can be then used to compute $c_{ij}$ which is the inter-individual covariance terms providing a measure of the tendency of the $i$th and $j$th individuals to vary in the same genetic direction from the centroid. Finally, Smouse and Peakall [27] defined the coefficient for all pairs of individuals that are $h$ steps apart as the following formula;

$$r^{(h)} = \left( \sum_{i \neq j}^{N} x_{ij}^{(h)} c_{ij} \right) \Big/ \left( \sum_{i=1}^{N} x_{ii}^{(h)} c_{ii} \right)$$

where $x_{ij}^{(h)} = 1$ for all pairs of individuals ($i$ and $j$) that are $h$ spatial distance classes apart, and $x_{ij}^{(h)} = 0$ otherwise. The coefficient $r$ is a proper correlation coefficient, with a mean of zero when there is no autocorrelation, and bounded by [−1, +1]. GenAlEx [23] offers then tests for statistical significance, based on two methods with 999 permutations respectively: (*i*) random permutation and (*ii*) bootstrap estimates of $r$.

## 3. RESULTS

The number of samples from each plot is listed in Table I. The average PIC value with three markers in the four plots was 0.8065, and the EP with six markers for the first parent in plot A was 0.9967. The differences in genotypes among adult trees allowed every adult to be discriminated from other trees. There were also many uncharacterized seed dispersal events due to the lack of endocarps to genotype or seed dispersal from outside the plot, but we identified mother trees of 62 seedlings in plot A following the method described above. In plot B, 108 seedlings matched just one adult. In addition, three seedlings each matched two adults at the three markers, but the true mother trees of these seedlings was identified from their respective candidates using the other three markers. Similarly, mother trees of 79 and 83 seedlings were identified in plots C and D, respectively, using just the three markers.

The mean spatial vector of seed dispersal was ($x$ = +3.84 m, $y$ = −6.77 m, $z$ = −5.07 m) in plot A, ($x$ = −1.95 m, $y$ = −5.63 m, $z$ = −3.18 m) in plot B, ($x$ = +7.14 m, $y$ = −4.92 m, $z$ = −0.14 m) in plot C, and ($x$ = +1.66 m, $y$ = +0.24 m, $z$ = −0.26 m) in plot D. The mean horizontal seed dispersal distances were 16.84, 10.38, 12.94 and 4.84 m

**Table II.** Mean horizontal and vertical seed dispersal distances, and spatial autocorrelation coefficients [23] for multilocus genotypes of adults ($r_a$) and seedlings ($r_s$) at the 5 m scale, together with the probability of [$r_a$ or $r_s$ > permutated $r$] in the four *Quercus crispula* plots.

| | Plot A | Plot B | Plot C | Plot D |
|---|---|---|---|---|
| Mean horizontal seed dispersal distance (m)* | 16.84 (11.05) | 10.38 (7.96) | 12.94 (10.01) | 4.84 (3.45) |
| Mean vertical seed dispersal distance (m)* | –5.07 (11.57) | –3.18 (3.44) | –0.14 (3.09) | –0.26 (9.59) |
| Autocorrelation coefficient ($r_a$) at 5 m scale (adult) | 0.06 | 0.04 | 0.05 | 0.00 |
| Probability of ($r_a$ > permutated $r$) | 0.128 | 0.029 | 0.078 | 1.000 |
| Autocorrelation coefficient ($r_s$) at 5 m scale (seedling) | 0.04 | 0.05 | 0.12 | 0.10 |
| Probability of ($r_s$ > permutated $r$) | 0.014 | 0.001 | 0.001 | 0.001 |

* The value in parenthesis indicates standard deviation.

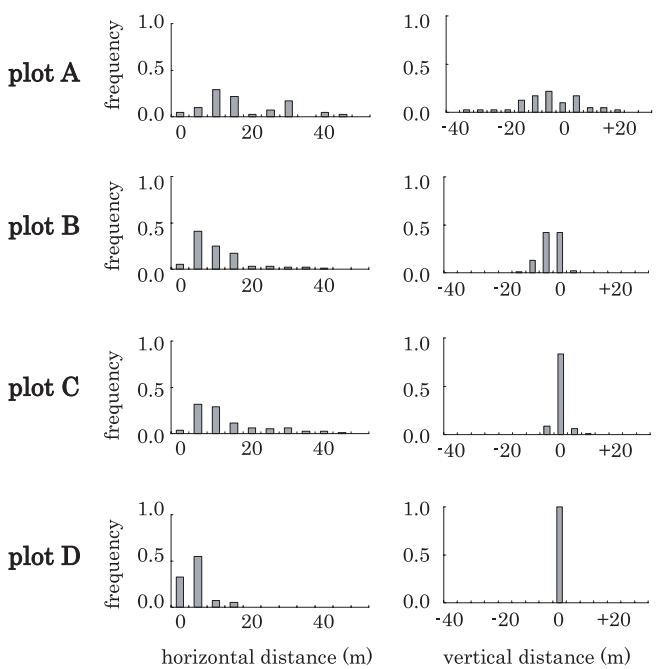


**Figure 2.** Distributions of seed dispersal distances along horizontal and vertical axes in four *Q. crispula* plots. The minus and plus in vertical distance mean downward and upward dispersals respectively.

in plots A, B, C, and D, respectively (Tab. II). The distributions of horizontal and vertical distances tended to be more widen on steeper sites (Fig. 2). Addition to this, the distribution of vertical distance biased left in plots A and B. Two typical examples of seed dispersal on slopes are shown in Figures 3 and 4 (for plots A and B, respectively). Most seeds were dispersed downwards, and the routes of some dispersed seeds crossed. A few upward seed dispersal events were also detected in plots A, B, and C. As illustrated in these figures, eleven out of 12 upward dispersal events detected in plot A and five out of 11 in plot B involved movement beyond the crown projections of the mother trees.

There were no clear trends in the autocorrelation coefficients for the adults, but the autocorrelation coefficients of first-year seedlings at the 5 m scale were 0.04, 0.05, 0.12 and 0.10 in plots A, B, C and D, respectively (Tab. II). Therefore, the coefficients were low on steep slopes, while they were relatively high on gentle slopes. But the probability for the autocorrelation coefficient to be greater than that which would be expected among a random sample from the sampled individuals, was less than 0.05 in every plot.

## 4. DISCUSSION

Both the PIC and EP of the microsatellite markers used was high enough to identify the mother trees of seedlings, and we detected evidence of both upward and downward dispersal events. The relatively large movement along $x$ axis in plot C might be attributed to the influence of strong winds from west. But on the whole, distributions of seed dispersal distances suggest that movements of most seeds were limited along horizontal and vertical axes in plots C and D on gentle slopes, but that many seeds were dispersed downwards in plots A and B on steep slopes. This is the most likely reason for why both the mean vertical and horizontal dispersed distances were much greater in plot A, on the steepest slope, than in the other plots. Large proportions of seeds (35%) in plot B flowed from outside the plot, which may also be due to the topographical slope. However, evidence of upward dispersal was often detected even in plot A on the steep slope. We cannot definitively determine the cause of the upward dispersal from our data, but upward dispersal within the crown projection of the mother trees was probably mediated by gravity. However, evidence of long upward dispersal beyond crown projections of the mother trees was also found, and such dispersal is more likely to be mediated by animals than by gravity. Both rodents and birds are known to transport *Q. crispula* seeds [20, 36]. However, rodents generally move oak seeds horizontally or downhill to conserve energy [18], and birds are the most likely to move seeds upwards. In support of this hypothesis, upward bird-mediated dispersal of seeds of various other species has been observed. For example, nutcrackers (*Nucifraga caryocataactes*) often transport seeds of beech (*Fagus crenata*), allowing *F. crenata* to immigrate into alpine zones or other high-altitude areas [36].

The spatial genetic structure of the adult populations of *Q. crispula* seemed to have no relation with topographical

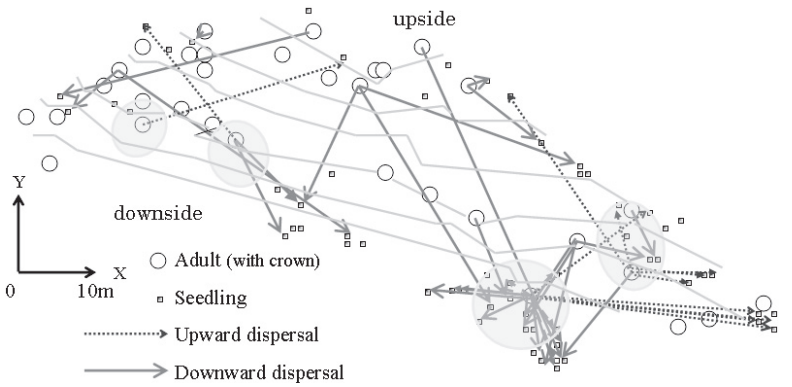


**Figure 3.** Seed flow, estimated from the adult and seedling genotype analysis in plot A. Contour lines are shown with intervals of 5 m. The crown projections (hatched areas) are shown for mother trees whose seeds were dispersed upwards.

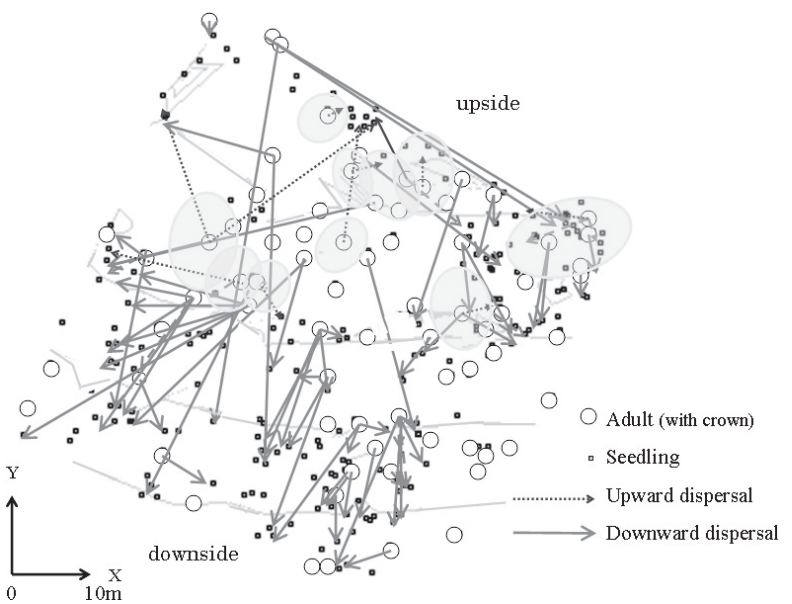


**Figure 4.** Seed flow, estimated from the adult and seedling genotype analysis in plot B. Contour lines are shown with intervals of 5 m. The crown projections (hatched areas) are shown for mother trees whose seeds were dispersed upward.

slopes. However, this may have been because the number of adults varied among the plots and the numbers of samples may have been too low in some cases for reliable evaluation of spatial genetic structure in these populations [15]. Therefore, the difference in the results among plots may reflect differences in sample size. For this reason the seedling data may be more suitable for detecting relationships between genetic structure and topographical slopes since more seedlings were sampled than adults. Accordingly, larger spatial autocorrelations amongst the seedlings were found on gentler slopes, despite the differences in the numbers of seedlings sampled in each plot. In other words, neighboring seedlings are more likely to be related to each other on gentle slopes than on steeper slopes. This is because most seeds are likely to be dispersed within limited areas on gentle slopes, as reported in several previous studies [16, 17, 33]. For example, Jones et al. [16] found that the spatial autocorrelation coefficient ($r$) for *Quercus rubra* seedlings at the 5 m scale was around 0.20 in a $40 \times 80$ m plot on flat ground in an aspen-white pine forest in northern Michigan, USA. However, many seeds were dispersed relatively long distances from their mother trees on the steep slopes we investigated, so low spatial autocorrelation coefficients were found there. Another factor that may have contributed to the weakness of the genetic structure on the steep slopes was that the dispersal routes of some of the seeds crossed, thereby merging the seed shadows of the mother trees.

In conclusion, most seeds of *Q. crispula* are dispersed downhill on steep slopes. Thus, neighboring seedlings are less likely to be related to each other than those on flat sites, although we found no relation between the genetic structure (patchiness) of the adult populations and the topographical slopes. In this study, we collected data only for *Q. crispula*, but similar phenomena may affect other tree species whose seeds

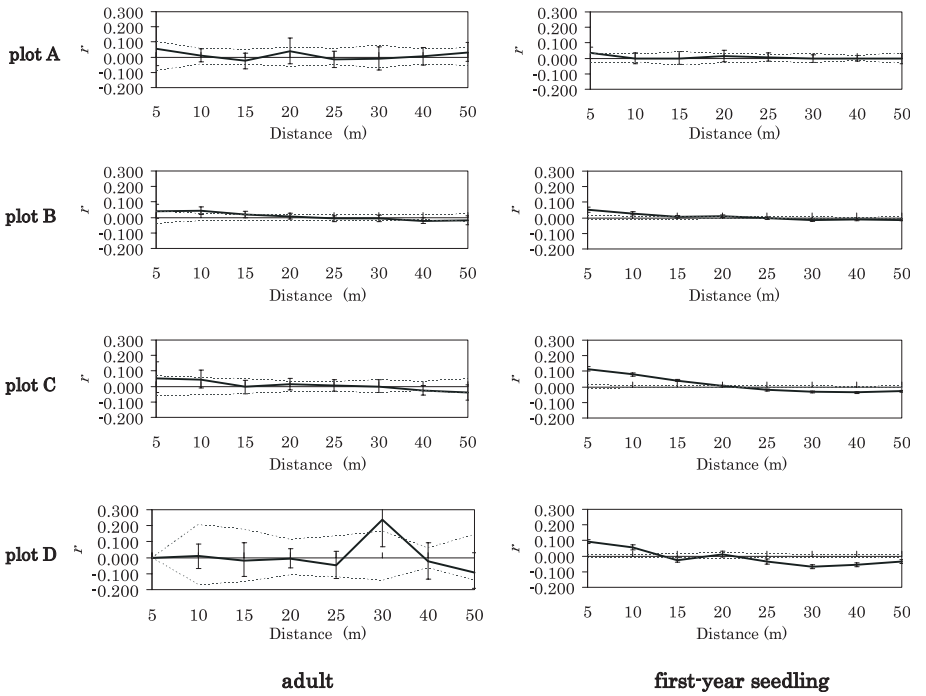


**Figure 5.** Correlograms of spatial autocorrelation ($r$) of adults (left column) and first-year seedlings (right column) for multilocus genotypes based on genetic distance methods [23] in four *Q. crispula* plots, with error bars showing the 95% confidence interval about $r$ as determined by bootstrap resampling. The two dotted lines in each correlogram show the 95% confidence intervals for the null hypothesis of no spatial structure derived from the combined data set.

are dispersed by gravity. Therefore, more research is needed to fully understand the effects of topographical slopes on the seed dispersal and genetic structure of trees.

**Acknowledgements:** Dr. K. Ishida, of the Graduate School of Agricultural and Life Sciences, the University of Tokyo, provided survey references and helpful advice. We are pleased to acknowledge the permission granted by Dr. S. Ishibashi, the chief of the University of Tokyo's Forest in Chichibu, and Dr. M. Kaji, the former chief, for us to take samples. Mr. Y. Watano, Mr. M. Takagaki, Mr. K. Uchiyama, and Mr. B. Wong, the laboratory of Forest Ecosystem Studies, helped with our sampling. We wish to thank everyone mentioned above.

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