Intraspecific variation of acorn traits of *Quercus serrata* Thunb. in Kanto region, central Japan

Yuko IWABUCHI1*, Yoshinobu HOSHINO2 and Tukasa HUKUSIMA2

Acorns (nuts and cupules) of 88 *Quercus serrata* Thunb. individuals in central Japan were collected in 2000 and 2001, and the relationships between twelve acorn traits and several environmental factors, such as altitude, warmth index (WI), annual mean temperature and precipitation were examined. All nut traits, three cupule traits and a peduncle trait were correlated negatively with altitude and precipitation during the acorn growing season, and positively with WI and annual mean temperature. These results indicated that the higher the precipitation was and the lower the WI, the smaller were the size and volume of nuts and cupules. This suggests that the differences in the length of the acorn growing season among the sampling sites may be responsible for the trends in acorn size and volume. The acorn size traits of *Q. serrata* were negatively correlated with precipitation during the acorn growing season, especially within the latter part of the growing season. Thus, we conclude that acorn size of *Q. serrata* had some strong relationship to less precipitation in the latter part of the acorn growing season. However, it was difficult to separate the effects of precipitation from those of temperature on acorn traits in our analysis. Moreover, *Q. serrata* nut length was more dependent on thermal conditions than was nut width. This difference may be caused by the different developmental patterns between these two dimensions, especially after August when the width stopped increasing but the length did not.

**Key words:** acorn traits, altitude, developmental pattern, precipitation, thermal condition

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**INTRODUCTION**

Seed size is one of the functional characteristics of plants and is closely related to plant strategies for maintaining populations under various environmental conditions. Harper et al. (1970) and Primack & Antonovics (1981) reported the constancy of seed size and weight within species, in contrast with the other organs of plants. Many studies, however, have described variations in seed size and morphology within woody and herbaceous plant species (Janzen 1978; Dorne 1981; Howe & Richter 1982; Petelka et al. 1983; Marshall et al. 1985; Daws et al. 2004) and examined the relationship between seed size and seed germination rate or seedling properties under field and experimental conditions (McComb 1934; Zimmerman & Weis 1983; Stanton 1984; Tripathi & Khan 1990). Moreover, some researchers have shown the relationship between seed size variations and environmental factors at a population or community level for woody and herbaceous plant species (McWilliams et al. 1968; Baker 1972; Schimpf 1977; Aizen & Woodcock 1992; Hiura et al. 1997) or the patterns of resource allocation toward reproduction in maternal plants (Cavers & Steel 1984; Wulff 1986).

The genus *Quercus* (Fagaceae) contains 300–500 species around the world (Moore 1984). In Japan, *Quercus* subgenus *Lepidobalanus* consists of seven species, one of which is evergreen and the other six deciduous. These species require one or two growing seasons for the maturation of their fruits (Kitamura & Horikawa 1951). *Quercus serrata* Thunb. is one of the deciduous broadleaf oak trees, and its fruit matures in one year. It is the common dominant species of secondary forests in warm and cool temperate zones of Japan. Its geographical distribution ranges from the southern part of Hokkaido to Kyushu, and from 20 to 1200 m above sea level in central Japan, where *Q. serrata* has the widest vertical distribution in Japan (Tsuji 2001).

The intraspecific seed (acorn) size variations in several *Quercus* species have been reported. Aizen & Woodcock (1992) studied the acorn size variations of 32 *Quercus* species in eastern North America. Similarly, the acorn...
size variations of *Quercus crispula* Blume from Hokkaido to southwest Japan were reported by Hiura et al. (1997). These studies suggested intraspecific geographical trends in acorn size. That is, the higher the latitude or the lower the warmth index (WI: Kira 1948), the smaller were the acorn volume and weight, and it suggests that the differences in the length of the acorn growing season at different sites affect the acorn size of *Quercus* species. Although it is well known that *Q. serrata* has acorn size variations (Abe et al. 1997), there is no study on the correlation between its acorn size variations and environmental factors in Japan.

In this paper we aim to examine the relationship between acorn traits (length, width, and volume) of *Q. serrata* and environmental factors in the Kanto region of central Japan.

### MATERIALS AND METHODS

#### Materials

Nuts and cupules of 88 *Quercus serrata* individuals (31 in 2000 and 57 in 2001) growing in six prefectures: Kanagawa, Tokyo, Saitama, Gunma, Tochigi and Yamanashi (Fig. 1), were collected along a latitudinal cline. In this region, natural crossing may be possible among individuals or populations, which largely exclude genetic differences in sampled individuals. The altitudes of the sampling sites in both 2000 and 2001 ranged from 60 to 1100 m above sea level. The annual mean temperatures of these sites ranged from 9.3–15.4°C, and WI from 71.7–124.2°C-month, nearly corresponding to the upper-half of the warm-temperate deciduous forest zone and the lower-half of the cool temperate broad-leaved forest zone (Nozaki & Okutomi 1990). The annual precipitation ranged from 1088 to 2397 mm (Japan Meteorological Agency 1996).

Brown-colored mature nuts and cupules were separately collected from the ground under the canopy of each sampled mother tree. It is known that the acorns of *Q. serrata* suffer insect damage throughout the growing season (Matsuda 1982). To remove the damaged acorns, the nuts were placed in water, and those that sank were selected as sound ones. Only sound acorns were used for our analysis. At least 10 sound nuts and 10 cupules were sampled per mother tree, and the largest number of samples of nuts, cupules, and cupules with peduncles contained 42, 57, and 42 in 2000, and 69, 84, and 64 in 2001, respectively.

#### Methods

A total of nine traits of nuts, cupules and peduncles were measured by a digital micrometer (Mitutoyo Co., Ltd.). Fig. 2 shows the measured parts of the nut (A–D), cupule (E–G) and peduncle (H–I): nut length, A; length from

![Fig. 1. Location of the study area in Kanto region, central Japan and sampling sites of *Quercus serrata* acorns. Acorns from 88 mother trees were collected in total.](image)

![Fig. 2. Measured parts of nut, cupule and peduncle. Nut length, A; length from the bottom to the widest point of the nut, B; nut width, C; width of the junction to the cupule, D; cupule width, E; cupule depth, F; width of the junction to the nut, G; peduncle length, H; peduncle width, I.](image)
the bottom to the widest point of the nut, B; nut width, C; width of the juncture to the cupule, D; cupule width, E; cupule depth, F; width of the juncture to the nut, G; peduncle length, H; peduncle width, I. The indices of nut volume, J\((A \times C^2)\); cupule volume, K\((E \times F^2)\); and peduncle volume, L\((H \times F)\) were calculated.

We examined the correlations between twelve acorn traits and several environmental factors at each sampling site, such as altitude, WI and precipitation. The meteorological data were obtained from Japan Meteorological Agency (1996). The WI was calculated as follows: 
\[ WI = \Sigma (T - 5) \]
where \(T\) is the monthly mean temperature above 5°C.

Since not all the values, as well as the log-transformed ones, fit the normal distribution curve well, we analyzed the correlation between the medians of twelve acorn traits per mother tree and five environmental factors at each sampling site.

## RESULTS

### Variations in acorn traits

Table 1 shows the medians and coefficients of variation \((CV)\) of the twelve acorn traits of 88 mother trees. Traits H, J, K, and L had larger \(CV\) values \((\geq 33.77\%)\) than the other traits \((\leq 19.06\%)\). Among the length traits, peduncle length (trait H) was more variable than the other traits.

### Correlations between acorn traits and environmental factors

The correlations between acorn traits and environmental factors were examined by the correlation coefficients. Each nut trait (A, B, C, D, J) had a significant negative relationship to altitude and a positive relationship to WI and annual mean temperature (Table 2, Fig. 3). Among five of the nut traits (A-D, J), nut length (A), length from the bottom to the widest point of the nut (B) and nut volume (J) showed higher correlation coefficient values than nut width (C) and width of the juncture to the cupule (D) (Table 2). None of the nut traits were correlated with annual precipitation except for nut width (C) and nut volume (J). However, all nut traits were correlated negatively with the precipitation during the acorn growing season. Thus, nut traits had a significant relationship to altitude, WI, annual mean temperature and the precipitation during the acorn growing season, and moreover, altitude, WI and annual mean temperature more strongly affected nut length (traits A and B) than nut width (traits C and D), although nut width traits were affected by the precipitation more strongly than nut length traits.

Three cupule traits (E, G, K) were correlated negatively with altitude and the precipitation during the acorn growing season, and were correlated positively with WI. None of the cupule traits were correlated with annual precipitation, except for cupule volume (K). Cupule depth (F) had no significant relationship to the environmental factors examined (Table 2, Fig. 3).

Two peduncle traits (H, I) were correlated with altitude and WI, but there was no significant relationship between peduncle length (H) and WI. Peduncle width (I) was correlated positively with altitude and negatively with WI, and peduncle length (H) had the converse trend with altitude. These traits had no significant relationship to both annual precipitation and precipitation during the

### Table 1

<table>
<thead>
<tr>
<th>Length traits</th>
<th>Median (mm)</th>
<th>CV (%)</th>
<th>Volume traits</th>
<th>Median (mm²)</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nut A</td>
<td>20.17</td>
<td>12.74</td>
<td>Nut J ((A \times C^2))</td>
<td>2561.34</td>
<td>33.77</td>
</tr>
<tr>
<td>B</td>
<td>10.42</td>
<td>15.86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>11.27</td>
<td>12.02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>5.00</td>
<td>12.69</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cupule E</td>
<td>10.16</td>
<td>11.91</td>
<td>Cupule K ((E \times F^2))</td>
<td>718.94</td>
<td>39.04</td>
</tr>
<tr>
<td>F</td>
<td>6.99</td>
<td>19.06</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>4.80</td>
<td>12.50</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peduncle H</td>
<td>8.59</td>
<td>36.05</td>
<td>Peduncle L ((H \times F))</td>
<td>21.60</td>
<td>44.97</td>
</tr>
<tr>
<td>I</td>
<td>1.59</td>
<td>17.41</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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Fig. 3. The relationship between environmental factors and acorn traits: A: length, B: width, C: width of the juncture to the cupule, D: width of the juncture to the nut, G: peduncle length, H. The r value shows the correlation coefficient between each trait and each environmental factor. ***: $P<0.001$, *: $P<0.05$.

acorn growing season. Peduncle volume (L) had no significant relationship to the environmental factors examined (Table 2, Fig. 3).

Correlations between acorn traits and moisture environments

Table 3 showed the correlations between the selected acorn traits (A–E, G, J, K) that were correlated with precipitation during the acorn growing season (from May to September, Table 2) and several moisture environmental conditions. Almost all of the nut and cupule traits had a significant relationship to the monthly precipitation from July to September, the latter part of the acorn growing season. Further, these traits had no significant relationship to either the acorn germinating and rootling season (from October to November) or the epicotyl's dormant season (from November to March) (Table 3).

### DISCUSSION

Intraspecific variation of acorn size

The coefficient of variation (CV) of peduncle length (H) was larger than those of the other 8 length traits (A–G and I), however, it was almost entirely uncorrelated with the environmental factors examined (Table 2). Thus, the variation in peduncle length may be attributed to hereditary variation within species, while most of the nut and cupule traits (except F) with low CV values varied with the environmental factors at each sampling site.

Although some traits, such as cupule depth (trait F) and peduncle volume (trait L), have no correlation with five environmental factors (Table 2), the acorn traits of *Q. serrata* in the Kanto region show intraspecific variations corresponding to the environmental factors examined. In our study, altitude, WI, and precipitation during the acorn growing season were significantly correlated with each other (Altitude–WI, $r=-0.903$, $P<0.001$; Altitude–Precipitation, $r=-0.508$, $P<0.001$; WI–Precipitation, $r=-0.609$, $P<0.001$). These results indicate that the lower the WI and the higher precipitation, the smaller are the size and volume of nuts and cupules.

The intraspecific variations of *Quercus* acorn were reported in eastern North America (Aizen & Woodcock 1992) and Japan (Hiura et al. 1997). Aizen & Woodcock (1992) showed significant negative correlations between latitude and intraspecific variation of acorn volumes of half
Table 2. The correlation coefficients between the medians of 12 acorn traits (A-L) and five environmental factors at each sampling site.

<table>
<thead>
<tr>
<th>Environmental factors</th>
<th>Nut</th>
<th></th>
<th></th>
<th>Cupule</th>
<th></th>
<th></th>
<th>Peduncle</th>
<th>Volume trait</th>
<th>Length traits</th>
<th>Volume trait</th>
<th>Length traits</th>
<th>Volume trait</th>
<th>Length traits</th>
<th>Volume trait</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (m)</td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
<td>J</td>
<td>E</td>
<td>F</td>
<td>G</td>
<td>K</td>
<td>H</td>
<td>I</td>
<td>L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.508***</td>
<td>-0.466***</td>
<td>-0.384***</td>
<td>0.346**</td>
<td>-0.460***</td>
<td>-0.318**</td>
<td>-0.100**</td>
<td>-0.361**</td>
<td>-0.259*</td>
<td>-0.245*</td>
<td>-0.256*</td>
<td>-0.053**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WI (°C-month)</td>
<td>0.461***</td>
<td>0.419***</td>
<td>0.365***</td>
<td>0.361***</td>
<td>0.428***</td>
<td>0.326**</td>
<td>0.111ns</td>
<td>0.429***</td>
<td>0.269*</td>
<td>0.147ns</td>
<td>-0.244*</td>
<td>-0.004ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual mean temperature (°C)</td>
<td>0.458***</td>
<td>0.415***</td>
<td>0.358***</td>
<td>0.350**</td>
<td>0.421***</td>
<td>0.315**</td>
<td>0.108ns</td>
<td>0.424***</td>
<td>0.260*</td>
<td>0.145ns</td>
<td>-0.254*</td>
<td>-0.014ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual precipitation (mm)</td>
<td>-0.165ns</td>
<td>-0.153ns</td>
<td>-0.222*</td>
<td>-0.218ns</td>
<td>-0.231*</td>
<td>-0.214ns</td>
<td>-0.133ns</td>
<td>-0.195ns</td>
<td>-0.231*</td>
<td>-0.151ns</td>
<td>0.055ns</td>
<td>-0.081ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation from May to September (mm)</td>
<td>-0.322**</td>
<td>-0.265*</td>
<td>-0.368***</td>
<td>-0.401***</td>
<td>-0.395***</td>
<td>-0.352**</td>
<td>-0.131ns</td>
<td>-0.393***</td>
<td>-0.304**</td>
<td>-0.117ns</td>
<td>0.031ns</td>
<td>-0.107ns</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Abbreviations refer to Table 1. ***: P<0.001, **: P<0.01, *: P<0.05, n.s.: not significant.

Table 3. The correlation coefficients between the medians of 8 acorn traits (A-E, G, J and K) and the precipitation data at each sampling site.

<table>
<thead>
<tr>
<th>Precipitation</th>
<th>Nut</th>
<th></th>
<th></th>
<th>Cupule</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
<td>E</td>
<td>F</td>
<td>G</td>
</tr>
<tr>
<td>Acorn growing season (from May to September)</td>
<td>-0.322**</td>
<td>-0.265*</td>
<td>-0.368***</td>
<td>-0.401***</td>
<td>-0.395***</td>
<td>-0.352**</td>
<td>-0.393***</td>
</tr>
<tr>
<td>May</td>
<td>-0.047ns</td>
<td>-0.030ns</td>
<td>-0.057ns</td>
<td>-0.070ns</td>
<td>-0.065ns</td>
<td>-0.078ns</td>
<td>-0.111ns</td>
</tr>
<tr>
<td>June</td>
<td>-0.190ns</td>
<td>-0.163ns</td>
<td>-0.250*</td>
<td>-0.243*</td>
<td>-0.255*</td>
<td>-0.207ns</td>
<td>-0.209ns</td>
</tr>
<tr>
<td>July</td>
<td>-0.362***</td>
<td>-0.299**</td>
<td>-0.387***</td>
<td>-0.438***</td>
<td>-0.431***</td>
<td>-0.366***</td>
<td>-0.429***</td>
</tr>
<tr>
<td>August</td>
<td>-0.419***</td>
<td>-0.358**</td>
<td>-0.438***</td>
<td>-0.472***</td>
<td>-0.480***</td>
<td>-0.415***</td>
<td>-0.468***</td>
</tr>
<tr>
<td>September</td>
<td>-0.278*</td>
<td>-0.205ns</td>
<td>-0.371***</td>
<td>-0.415***</td>
<td>-0.376***</td>
<td>-0.375***</td>
<td>-0.396***</td>
</tr>
<tr>
<td>Acorn germinating and rooting season (from October to November)</td>
<td>0.056ns</td>
<td>0.049ns</td>
<td>0.003ns</td>
<td>0.078ns</td>
<td>0.025ns</td>
<td>0.004ns</td>
<td>0.159ns</td>
</tr>
<tr>
<td>Epicotyl's dormant season (from November to March)</td>
<td>0.177ns</td>
<td>0.095ns</td>
<td>0.126ns</td>
<td>0.173ns</td>
<td>0.145ns</td>
<td>0.113ns</td>
<td>0.194ns</td>
</tr>
</tbody>
</table>

*Abbreviations refer to Table 1. ***: P<0.001, **: P<0.01, *: P<0.05, n.s.: not significant.
of 32 Quercus species examined. In Japan, the acorn weight of Quercus crispula had a significant positive relationship to WI of each of the sampling sites (Hiura et al. 1997). These studies suggested that geographical trends of thermal conditions led to differences in the length of the growing season among sampling sites, which in turn caused the variations in acorn volume and weight. The altitudinal trends of acorn traits in our study showed that all nut traits, cupule width and cupule volume of Q. serrata were smaller at higher altitudes. The length of the acorn growing season in higher altitudinal regions was shorter than in lower altitudinal regions because of the later flowering (Sasaki 1983) and the earlier leaf fall. Therefore, the differences in the length of the acorn growing season among the sampling sites may be responsible for the trends in Q. serrata acorn size, similar to the results of Aizen & Woodcock (1992) and Hiura et al. (1997).

Acorn size and drought stress

Schimpf (1977) reported significant negative correlations between moisture availability in an environment and seed size of Amaranthus retroflexus populations in North America, and Baker (1972) reported a similar result for seed size of California herbs. They showed that larger seed size is important to establish seedlings in a drought environment, because large seeds could develop large root systems extending deeply into the soil. Further, McComb (1934) reported that the root weight of chestnut oak's (Quercus montana Willd.) seedlings were positively correlated with the acorn weight. Thus, we consider that the root size of Q. serrata seedlings may be correlated positively with their acorn size, as with Q. montana seedlings, and that viability of acorns germinating just after fall may depend on their size. Additionally, Hiroki & Matsubara (1982) reported that the autumn and winter desiccation in the lower precipitation areas of Japan increased the mortality of current year Q. serrata acorns with radicle and epicotyl in dormant, even buried in the litter. Therefore, a further question has arisen as to which drought stress is correlated with acorn size of Q. serrata in this study site.

The acorn size traits (all nut traits, cupule width and cupule volume) were negatively correlated with precipitation during the acorn growing season, especially with that in the latter part of the growing season (from July to September) (Table 3). On the other hand, our results showed that precipitation in both the acorn germinating and rooting season (from October to November) and epicotyl's dormant season (from November to March) had no influence on these traits. Thus, we conclude that acorn size of Q. serrata had some strong relationship to less precipitation in the latter part of the acorn growing season. However, it was difficult to separate the effects of precipitation from those of temperature on acorn traits in our analysis.

Mechanism underlying acorn size variation

Although acorn size was influenced by thermal conditions, the effects of such conditions varied from trait to trait, i.e., the correlation coefficients between nut length (traits A and B) and altitude or WI were higher than those between nut width (traits C and D) and altitude or WI. This suggests that nut length is more dependent on thermal conditions than nut width. Murphy & Frey (1962) studied the dependence of fruit traits of oat on environmental factors in relation to the developmental pattern of the fruit. According to them, oat fruit width required a longer period for full development than length, and this difference was responsible for width's higher dependence than length on environmental factors. Similarly, the developmental pattern of the width of Q. serrata acorn was different from that of length. Although both the width and length of an acorn begin to increase after fertilization, the width stopped increasing in August whereas the length continued to increase until late September, and moreover, acorn length increased drastically after August (Hashizume & Ozaki 1979; Matsuda 1982; Hashizume 1987). Thus, the dependence of nut length on thermal conditions is considered to result from the difference in the length of growing season, especially the length between August and the end of the growth season.

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要約
関東地方におけるコナラ（Quercus serrata Thunb.）の果実形態の種内変異。岩瀬拓子（東京農工大学大学院農学研究院）・星野義彦・福嶋司（東京農工大学農学部）
関東地方に生育するコナラ88個体の果実（堅果と殻）を2001,2002年に採集し、各果実形態について計測した12形質と、採集地点の環境要因（標高、暖かさの指数、年平均気温、降水量）との関係を調べた。堅果の全形質と殻の3形質、殻の柄の1形質は、標高および果実成長期間降水量との間に有意に負の相関を、暖かさの指数および年平均気温との間に有意な正の相関を示した。したがって、降水量が多くWI値が低地地域では、堅果、殻、殻の柄の形態が小さくなることが明らかになった。この果実形態にみられる傾向は、採集地点間での果実成長期間長の相違によるものであると考えた。コナラの果実形態を示す形質は、果実成長期の中でも成長期後期の降水量と有意な負の相関関係を示した。したがって、コナラの果実形態は、果実成長期後半の少降水量と強く関係することが明らかになった。しかし、本研究では、果実形態に対する湿度、降水量の影響を分析して解析することはできなかった。さらに、コナラの堅果長は殻果幅と共

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べて、温度条件に対してより高い依存性を持つことが明らかとなった。堅果長の温度条件への高い依存性は、8月以降堅果幅の成長が頭打ちになるのに対して、堅果長は8月以降にも成長を続けるという、発達パターンの違いによるものと考察した。