

Morphological variation along the sea-land gradient: trees in a subtropical maritime woodland

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Received: 3 July 2009 / Accepted: 16 April 2010 / Published online: 15 May 2010
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Abstract As long-lived sessile organisms, trees demonstrate morphological variability in response to the environmental conditions encountered in a particular local habitat. However, the detection of such variation on a small spatial scale may not be straightforward. In this study we investigated the morphological variation of trees along the edge–interior gradient of a small subtropical-temperate coastal woodland in Amakusa, western Kyushu, Japan. The woodland was located on a narrow sand-spit surrounded by the sea, thus exposed to intense marine influences. In three dominant tree species, *Quercus glauca*, *Ligustrum japonicum*, and *Pittosporum tobira*, the tendency of multi-stemming was significantly greater on the seaward edge of the woodland and declined towards the interior. Furthermore, tree height and size (cross-sectional area at breast height) declined and canopy openness increased towards the woodland edge. In *Q. glauca* and *L. japonicum*, shoot growth was more pronounced in the interior than on the edge (i.e. shorter shoots with wider spacing in the latter habitat). Thus, spatial variation in tree structure manifested clearly as shorter height with greater multi-stemming tendencies and greater canopy openness (more spacing among branches/shoots) towards the woodland edge where more light is available and the effects of sea wind and salt spray are greater.

Keywords Canopy openness · Edge–interior gradient · Multi-stemming tendency · Salt spray · Sea wind

Introduction

Coastal woodlands exist in an interface between terrestrial and marine environments, with marked environmental gradients. In particular, non-mangrove woodlands in subtropical-temperate coastal regions of East Asia tend to experience severe physical disturbances in the form of storms and typhoons (Naka 1982; Bellingham et al. 1996; Miura et al. 2001; Masaka and Sato 2002). In general, wind disturbance affects trees along the edge more severely than those in the interior sites of a woodland (Campbell 1998; Asquith and Mejia-Chang 2005), whereas light availability is greater towards the edge (Chen et al. 1999). Although these factors could affect the morphological characteristics of trees on relatively small spatial scales, there have been a limited number of empirical studies that have examined in detail morphological variation in a coastal tree assemblage (Nzunda et al. 2007).

Trees demonstrate morphological variation at different levels of structural organization:

1. whole tree characteristics including canopy height, canopy shape and multi-stemming patterns;
2. shoot shapes, sizes, and distribution of branches; and
3. leaf morphology.

Different aspects of these have previously been discussed in relation to wind stress (Lawton 1982; Foster 1988; Jaffe and Forbes 1993; Cordero et al. 2007), interspecific light competition (Kohyama 1993; Aarssen 1995), and light-capture efficiency (Sakai 1990; Niinemets and Kull 1995; Henry and Aarssen 1997; Stoll and Schmid 1998; Takahashi et al. 2001; Poorter et al. 2003, 2005, 2006; Seiwa et al. 2006). On the other hand, there is a paucity of information on how different aspects of morphology vary with an environmental gradient on small to

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medium spatial scales (<100 m). In the study by Nzunda et al. (2007) of a coastal sand dune forest, variation in tree height and multi-stemming tendency were observed on a spatial scale of 300 m.

This study looked into the pattern of morphological variation of trees in a small coastal woodland in south-western Japan. As this woodland is semi-isolated on a narrow sand spit surrounded by the sea (see below), it is exposed more directly to maritime influences than ordinary coastal forests and is, therefore, considered to demonstrate sharper morphological changes on a small spatial scale. We hypothesised that significant morphological trends would be detectable on a spatial scale of less than 50 m at the marine–terrestrial interface. We tested this by analysing the patterns of variation in whole-tree morphological characteristics, particularly the multi-stemming tendency, and shoot growth with reference to the woodland edge–interior gradient among the three major species occurring in this maritime woodland.

Materials and methods

Study site

The study site was located on the north-western corner of the Amakusa Shimoshima Island in Kyushu, south-western Japan (32°32'N, 130°02'E) (Fig. 1). The woodland occurs on a narrow sand spit projecting into the Ariake Sea, part of

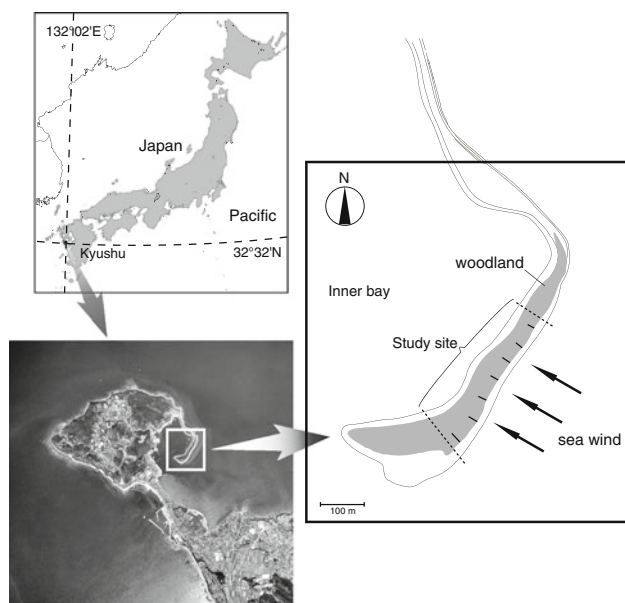


Fig. 1 Location of the study site. Transects are indicated in the study site. The aerial photograph was modified from the original supplied by the Geographical Survey Institute, Japan (<http://w3land.mlit.go.jp/WebGIS/>)

the East China Sea, covering a total area of 23300 m². The north-eastern-most point (500 m long) of this spit, 0–3.8 m above sea level, was chosen as the study site. At the time of the study, this site was partially isolated from the basal part of the spit by a narrow (ca. 10 m), barren gap where the seawater breached the land in the past. The eastern side of the study site was exposed to the effect of sea wind whereas the western side was more protected by steep coastal hills across a small enclosed bay. Therefore, a more marked marine–terrestrial interface occurred on the outer, eastern shore of the study site. The only source of fresh-water into this woodland is through precipitation. This region has been described as subtropical with summer surface water temperatures constantly reaching above 28°C (Kawai and Tokeshi 2004). According to the local meteorological record, a maximum momentary wind velocity of >20 m s⁻¹ occurred on 45 occasions between 1999 and 2004, including two occasions exceeding 50 m s⁻¹ (Japan Meteorological Agency <http://www.jma.go.jp/en/typh/>). Our preliminary survey revealed that three species, *Quercus glauca*, *Ligustrum japonicum*, and *Pittosporum tobira*, accounted for approximately 70% of tree individuals in the study site.

Field measurements

Because this study dealt with a gradient associated with the marine–terrestrial interface, observations were made on trees positioned between the woodland edge parallel to the outer (eastern) shoreline and the interior, 20–25 m from the edge (Fig. 1). A total of seven 10 m-wide transects were established perpendicular to the coastline at 50-m intervals. For the three dominant species *Quercus glauca*, *Ligustrum japonicum*, and *Pittosporum tobira*, the diameter at breast height (dbh, 1.3 m above the ground) and the distance from the edge of the woodland of each tree within the transects were recorded. This included all trees with dbh > 4 cm and those with multiple stems at breast height with total cross sectional area >12 cm². In the case of multiple stems, the circumference of each stem was measured. Size (*S*) of each tree was represented as a sum of cross-sectional area based on dbh, thus,

$$S = \sum_{i=1}^n (d_i/2)^2 \times \pi$$

where *d_i* is the diameter (at breast height) of the *i*th stem of a tree and *n* is the number of stems. Based on this size measure, tree abundance per area was evaluated as a combined *S* for all individuals of the same species in a quadrat of 5 m × 10 m. Further, morphological variation of trees from the edge to the interior was examined by calculating the multi-stemming index (*B*) for each tree:

$$B = \frac{\text{(number of stems at breast height)}}{\text{(total cross-sectional area)}}$$

This index enables comparison of multi-stemming tendencies while taking into account variation due to differences in tree size (most likely a reflection of age). Tree height was measured to the nearest 5 cm by use of an extendable measuring pole.

Shoot growth was measured in the edge and the interior (20–25 m) sites in spring–summer 2002. For this measurement, trees with open crown and under similar environmental conditions (i.e. receiving no or little shading from other trees) were selected (30 *Q. glauca*: 22 from the edge 8 from the interior, 29 *L. japonicum*: 11 from the edge and 18 from the interior). Unbalanced data sets were used between the edge and the interior site because of the limited number of trees under similar conditions, especially *Q. glauca* in the interior of the woodland. A total of 30 shoots in the most exposed positions on each tree were separately marked with number tags and the length (from the apex to the base of new growth) was measured to the nearest mm. *Pittosporum tobira* was excluded from this analysis because of its low density in the interior, being a shade-intolerant species.

Canopy openness is a useful measure of canopy structure (Weiss et al. 1991) and light availability (Rijkers et al. 2000). Data on canopy openness were collected by taking photographs at different distances (5-m intervals) from the edge to interior with a fish-eye lens attached to a digital camera (Englund et al. 2000) at 1 m height in winter (December) and summer (June). These photographs were assessed by use of the Canopon2 program (<http://take.naka-akio.cool.ne.jp/etc./canopon2/index.html>) and canopy openness was expressed as proportional values (i.e. estimated proportion of open areas over a hemispherical surface).

Data analysis

Statistical analyses were performed using Statview 5 (SAS Institute) and SPSS 11.5 (SPSS). Ordinary regression analysis was used to examine the tendency of change in tree morphology (size, height, and the multi-stem index), density and abundance along the edge–interior gradient. Logistic regression combined with Scheffé’s test was used for examining the canopy openness data. For comparing the differences in growth patterns of *Q. glauca* and *L. japonicum* between the edge and the interior, repeated measures ANOVA was applied to shoot-length data with nesting by tree individuals over the growth period. Nested ANOVA was also used to test the differences in maximum shoot lengths attained by trees in different habitats. Data were

subjected to logarithmic transformation (Zar 1996) where necessary. Untransformed means are reported in the results even if statistical tests were done using transformed data.

Results

Plotting of the index of multi-stemming against distance from the edge clearly demonstrated a decreasing trend of multi-stemming towards the interior (Fig. 2, regression analysis of log-transformed data, *Q. glauca*, $r^2 = 0.11$, $P < 0.0001$; *L. japonicum*, $r^2 = 0.07$, $P < 0.05$; *P. tobira*, $r^2 = 0.51$, $P < 0.0001$). In contrast, no significant trend was detected except for *P. tobira* between the number of stems at breast height and the distance from the woodland edge (Fig. 2, insets), because of the confounding effect of tree size variation.

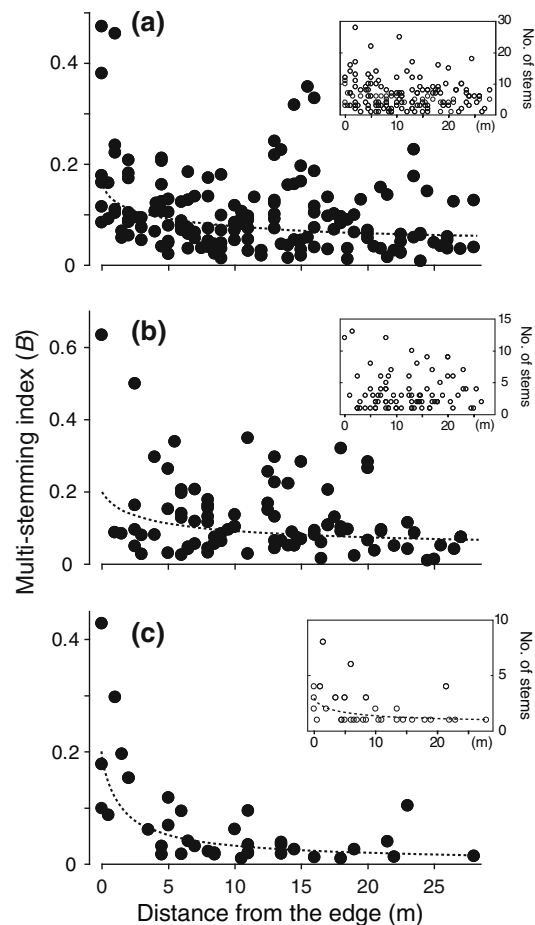


Fig. 2 Relationship between multi-stemming and distance from the edge. Multi-stemming index of **a** *Q. glauca*, **b** *L. japonicum*, **c** *P. tobira*. Fitted lines are **a** $y = 0.15x^{-0.30}$, $r^2 = 0.11$, $P < 0.0001$, $n = 158$; **b** $y = 0.20x^{-0.33}$, $r^2 = 0.07$, $P < 0.05$, $n = 88$; **c** $y = 0.20x^{-0.76}$, $r^2 = 0.51$, $P < 0.0001$, $n = 36$. Insets variation in the number of stems with distance, regressions not significant except for **c** $y = 3.0x^{-0.33}$, $r^2 = 0.24$, $P < 0.005$, $n = 36$

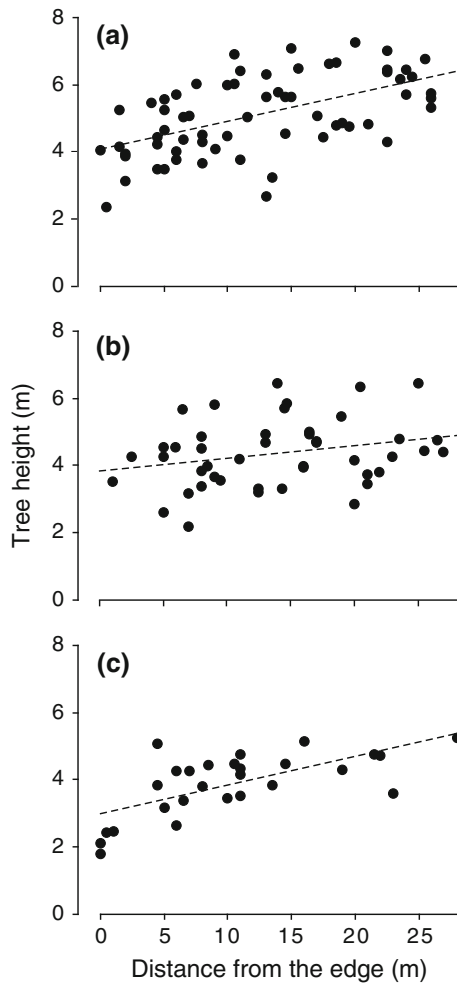


Fig. 3 Relationship between tree height and distance from the edge. Tree height of **a** *Q. glauca*, **b** *L. japonicum*, **c** *P. tobira*. Regression lines are **a** $y = 4.1 + 0.08x$, $r^2 = 0.30$, $P < 0.001$, $n = 64$; **b** $y = 3.8 + 0.038x$, $r^2 = 0.07$, $P = 0.08$, $n = 45$; **c** $y = 3.0 + 0.085x$, $r^2 = 0.44$, $P < 0.001$, $n = 27$

Tree height increased significantly towards the interior for *Q. glauca* and *P. tobira* (Fig. 3, *Q. glauca*, $r^2 = 0.30$, $P < 0.001$, *P. tobira*, $r^2 = 0.44$, $P < 0.001$), but the trend was marginal in *L. japonicum* ($r^2 = 0.07$, $P = 0.08$). Similarly, tree size represented by cross-sectional area at breast height also increased towards the interior (Fig. 4, *Q. glauca*, $r^2 = 0.04$, $P < 0.01$; *L. japonicum*, $r^2 = 0.05$, $P < 0.05$; *P. tobira*, $r^2 = 0.43$, $P < 0.001$).

Over the growth period in spring-early summer, both *Q. glauca* and *L. japonicum* showed greater shoot elongation in the interior than in the edge habitat (Fig. 5; repeated-measures ANOVA, *Q. glauca*: $F = 5.9$, $P < 0.05$; *L. japonicum*, $F = 4.6$, $P < 0.05$). *Quercus glauca* attained a significantly larger maximum shoot length in the interior (175.6 ± 20.6 (mean \pm SE) mm) than in the edge habitat (130.3 ± 7.8 mm) (ANOVA, $F = 5.2$, $P < 0.05$). Similarly, *L. japonicum* had a greater maximum shoot length in

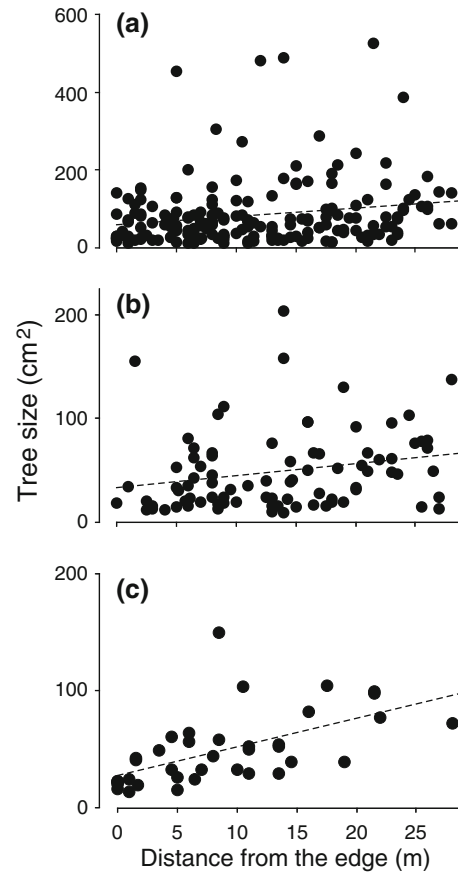


Fig. 4 Relationship between tree size and distance from the edge. **a** *Q. glauca*, **b** *L. japonicum*, **c** *P. tobira*. Regression lines are **a** $y = 59.5 + 2.1x$, $r^2 = 0.04$, $P < 0.01$, $n = 158$; **b** $y = 33.4 + 1.2x$, $r^2 = 0.05$, $P < 0.05$, $n = 88$; **c** $y = 27.5 + 2.4x$, $r^2 = 0.34$, $P = 0.0001$, $n = 36$

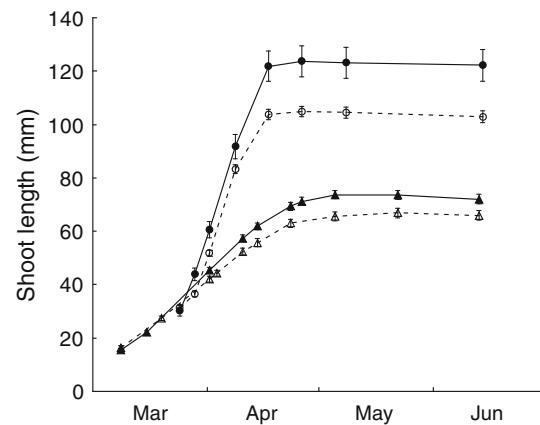


Fig. 5 Variation in shoot length of *Q. glauca* (circles) and *L. japonicum* (triangles) in the edge (open symbols) and in the interior (filled symbols) of the woodland

the interior than in the edge habitat (100.6 ± 5.6 vs. 87.1 ± 6.4 mm; ANOVA, $F = 4.6$, $P < 0.05$). Further, temporal variation in shoot growth pattern (rates) was

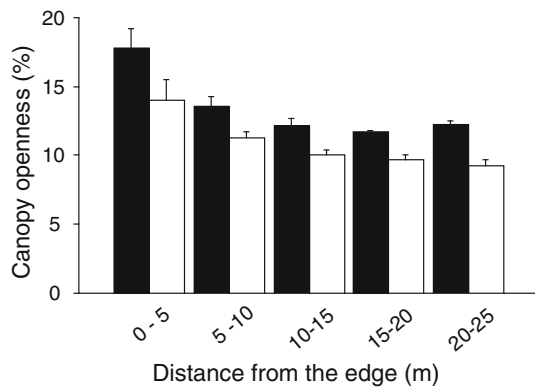


Fig. 6 Variation in canopy openness from the edge to the interior in December (filled bars) and June (open bars). Error bars +1 SE

significantly different between the sites, as confirmed by the interaction between sites and time in both species (repeated-measures ANOVA, *Q. glauca*, $F = 6.6$, $P < 0.01$; *L. japonicum*, $F = 6.3$, $P < 0.01$). Canopy openness showed a significant decline from the edge to the interior, especially in the first 5 m from the edge (Fig. 6, logistic regression analysis plus Scheffé's test, $r^2 = 0.37$, $P < 0.01$ (December); $r^2 = 0.19$, $P < 0.001$ (June)).

Discussion

Whereas previous studies on different woodland assemblages reported higher tree densities (Lawton 1984), lower height (Lawton 1982; King 1986; Meguro and Miyawaki 1994; Griffiths 2006), and smaller stem sizes (Lawton 1982; King 1986) under wind-exposed conditions, there is a paucity of information on multi-stemming tendencies in the context of an edge–interior gradient (Nzunda et al. 2007). Tree morphologies are affected by:

1. wind disturbances (Lawton 1982; Meguro and Miyawaki 1994; Van Bloem et al. 2003; Van Bloem and Murphy 2005); and
2. light availability on local scales (Kohyama 1987, 1991; Sakai 1990; Takahashi et al. 2001; Henry and Aarssen 1997; McDonald and Urban 2004)

but in practice it is difficult to recognise the effects of wind disturbances and light acquisition separately, because of the overlapping nature of wind/light exposure. Indeed, trees are likely to show adaptive morphological trade-offs with regard to:

1. lower light availability with reduced disturbances in the interior; and
2. greater light availability with frequent disturbances in the woodland edge.

This study concurs with that of Nzunda et al. (2007) on a coastal sand dune forest, demonstrating the morphological variation of trees, particularly a multi-stemming tendency, along an interior-to-edge gradient of a maritime woodland. It is notable, however, that the spatial scale on which the morphological variation occurred (<30 m) is much smaller than in Nzunda et al. (2007), where a similar phenomenon occurred on the spatial scale of 300 m. Despite such scale differences, this morphological variation may largely constitute a summary response of trees to wind perturbations which are generally more pronounced towards the exposed woodland edge (Naka 1982; Tanner et al. 1991; Campbell 1998; Asquith and Mejia-Chang 2005). Previous studies have also reported that tree mortality is higher along the edge of forests (Lovejoy et al. 1984; Williams-Linera 1990; Bellingham et al. 1996; Chen and Franklin 1992; Campbell 1998; but see Lin et al. 2004) and consequently gap formation occurs more frequently (Kapos et al. 1993; Laurance 1997), leading to greater canopy openness (Williams-Linera 1990).

The fact that the three dominant tree species showed an increased tendency of multi-stemming towards the woodland edge must at least partially be related to wind stress, which is known to induce the sprouting of new branches even if physical damage is not apparently inflicted on stems (Van Bloem and Murphy 2005; Nzunda et al. 2007). Although stem breakages were observed occasionally after a storm in the study site, direct mechanical damage was unlikely to be responsible for the observed variation in tree height; the effect of non-damage-level wind is more probable in our view. That trees were shorter and thinner in the wind-exposed seaward edge is also consistent with similar observations in previous studies (Naka 1982; King 1986; Meguro and Miyawaki 1994; Campbell 1998; Miura et al. 2001; Peterson 2004; Van Bloem and Murphy 2005). Indeed, it is known that trees on wind-exposed mountain ridges adopt thin, elfin forms (Lawton 1982; Foster 1988). It has also been reported that sea wind disturbances tend to limit tree growth (Cordero 1999; Griffiths 2006). Consequently, shorter trees with more branched structures tend to dominate tree assemblages on the seaward edge of this coastal woodland.

Quercus glauca is capable of adopting a flexible growth strategy, involving a trade-off between height growth and stem-diameter growth depending on varying light conditions (Sumida et al. 1997). It is also notable that many *Q. glauca* individuals in this study had multi-stemming forms at a relatively low level (<50 cm) rather than at higher levels, which might be related to the fact that branching in *Q. glauca* can occur soon after the sapling stage (Cho et al. 2005), thus enabling the individuals of this species to have a variety of shapes.

These considerations suggest that there seems to occur a conflicting ecological situation concerning the determination of branch sizes of trees in the wind-exposed woodland edge, as higher irradiance due to greater canopy openness tends to encourage branch/shoot growth (in terms of thickness and length, Stoll and Schmid 1998; Umeki and Kikuzawa 2000; Sone et al. 2005; Takahashi et al. 2006), whereas wind perturbations at the edge tend to restrict branch/shoot growth and favour shorter, thinner branches and shoots which are less susceptible to mechanical stresses due to wind. Further, shoots exposed to strong irradiance and salt spray at the seaward edge need to invest more in the production and maintenance of leaves, including thicker leaf surfaces (Boyce 1954; Campbell 1998; Hanba et al. 2002; Zhu et al. 2002; Griffiths and Orians 2003; Griffiths 2006). Consequently, there may be an optimum branch/stem size under a given set of environmental conditions encountered with the maritime edge habitat.

In summary, this study demonstrates that on a small spatial scale of ~25 m along the woodland edge–interior gradient, morphological variations manifest themselves in the form of height, size, and multi-stem structures of the three dominant tree species. These are considered to result from their ecophysiological plasticity in the face of changing environmental conditions encountered in the sea–terrestrial interface of this maritime woodland. Shorter height with greater multi-stemming tendencies and shorter shoots coupled with greater canopy openness (more spacing between branches and shoots) towards the seaward edge are the responses that will enable efficient light capture and at the same time create environmental heterogeneity which is important for other organisms associated with these tree assemblages. Further, the observed spatial variation in tree morphology suggests that trees positioned successively from the edge to the interior can have direct and indirect effects on those positioned towards the interior, the details of which remain to be investigated.

Acknowledgments Thanks are due to Jusak R.P. Daud for help with field work and Takashi Kawai and Seiji Arakaki for advice at different stages of this work. MY is indebted to the past and present members of the Amakusa Marine Biological Laboratory, especially the late Masahiro Kido, for various forms of support during the course of this study. This work was supported financially by the Kyushu University P & P program, the twenty-first Century COE and the GCOE programs of the Ministry of Education, Culture, Sports, Science, and Technology and the scientific research grant (“Grant-In-Aid” nos 14340246 and 14255013 to MT) from the Japan Society for the Promotion of Science.

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