Tree coexistence on a slope: an adaptive significance of trunk inclination

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SUMMARY

Under storey trees on slopes often incline their trunks downwards. The adaptive significance of this conspicuous phenomenon has, however, remained elusive. Here we present a theoretical model for the growth of under storey trees on a slope, which shows that the maximum rate of tree survival, and the optimal degree of trunk inclination, increase as the slope gets steeper, clearly indicating an adaptive significance of trunk inclination on slopes. Close examination of the results reveals that the advantage of trunk inclination on a slope is in shortening the distance from the canopy surface, and that this effect is enhanced the steeper the slope. Furthermore, the model predicts that the maximum tree survival rate increases with the slope angle more sharply under poorer light conditions. The predictions of the model are supported by an under storey species, *Rhododendron tashiroi*, which grows in evergreen forests on the Japanese island of Yakushima. *R. tashiroi* exhibits sharper trunk inclination and coexists more successfully on steeper slopes with the dominant canopy species, *Distylium racemosum*, and sustains itself even under poor light conditions where the slope is sufficiently steep. This also suggests that trunk inclination is a mechanism used by under storey species to coexist with the dominant canopy species.

1. INTRODUCTION

Under storey trees on a slope often incline their trunks downwards. Two major explanations for this have been put forward: (i) that it is the consequence of disturbances on slopes, such as landslides (Del Tredici 1992; Shimada 1994; Sakai *et al.* 1995); (ii) that it is caused by wind (King 1981; Putz *et al.* 1983; Mattheck 1991). However, these explanations, both of which implicate passive processes caused by external physical forces, have shortcomings: the former explanation cannot account for the tendency of trunk inclination to be confined to under storey species, while the latter cannot explain why this phenomenon is observed more often on slopes. Umeki (1995), on the other hand, suggests that trunk inclination on slopes may be an active response of trees.

Two related questions arise concerning this tendency of under storey trees on slopes to incline their trunks downwards: (i) is there any adaptive significance of trunk inclination for under storey trees on slopes? (ii) does trunk inclination help under storey species to coexist with the canopy species on slopes?

To investigate these questions, we first construct a theoretical model for the growth process of an under storey tree under the canopy structure on a slope, and test the model predictions against the data from a field study in evergreen forests on Yakushima, an island located in the south-western part of Japan.

2. THE MODEL

The model describes a tree growing in a forest (of canopy height h) on a slope making an angle θ with the horizon (figure 1*a*). When the tree has length l and inclines downward by an angle α , the distance of its crown top from the canopy surface is given as

$$z = h - l(\cos \alpha + \sin \alpha \tan \theta), \quad (1)$$

which, given h and l , decreases with an increase in either trunk inclination (α ($0^\circ \leq \alpha < \theta$)) or the slope angle (θ ($0^\circ \leq \theta < 90^\circ$)). Employing Beer–Lambert's Law, the light intensity at z is given as

$$I = I_0 e^{-\kappa z}, \quad (2)$$

where I_0 denotes the light intensity on the canopy surface and κ is the light extinction coefficient per unit depth (figure 1*a*).

The above ground part of the tree is assumed to have a columnar shape with length l and radius cl . Thus its volume is

$$V_t = \pi c^2 l^3, \quad (3)$$

where c is a constant coefficient representing the ratio of trunk radius to tree height. The more the tree inclines, the greater is the bending moment loaded by its weight. The tree therefore has to add supporting organs such as reaction wood and buttresses to avoid death caused by the trunk buckling. The volume of these supporting organs, V_s , can in general be assumed to be an increasing function of α and l . Specifically, we

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Figure 1. (a) Cartoon (not to scale) showing a side view of the model for a tree growing in a forest, on a slope, as described in the text. (b) Schematic representation of the model for the above ground part of the tree. The circle and the oval in left show the cross-sections of the column and the supported part of column, respectively. The half length of the major axis b corresponds to $b(x)$ in equation (5a).

assume that V_s is proportional to the volume of the reaction wood, V_r , so that

$$V_s = sV_r, \quad (4)$$

where s is a constant coefficient. Under the simplifying assumptions that the section of the trunk containing

the reaction wood has an oval shape and the wood has no elasticity, V_r can be evaluated by the following formula (Ishii, *in preparation*):

$$V_r = \pi c l \int_{l_a}^l b(x) dx - \pi c^2 l^2 (l - l_a), \quad (5a)$$

where $b(x)$ is the half length of the major axis of the oval cross section (b in figure 1), which satisfies:

$$\frac{32}{b(x)^2} \left(r \left(x - \frac{l_a}{2} \right) + \int_{l_a}^x b(t) (x-t) dt \right) = \sigma, \quad (5b)$$

$$l_a = \frac{1}{4} \sqrt{\left(\frac{cl\sigma}{D \sin \alpha} \right)}, \quad (5c)$$

where D , σ , and $(l-l_a)$ are the specific gravity of wood, the specific maximum allowable stress of wood, and the length of the reaction wood, respectively. It is known that the relation between D and σ is $\sigma = 83.1 + 1390D$ (Nakai & Yamai 1982).

Let the photosynthetic rate of the tree, P , be proportional to the crown volume, which is assumed to be proportional to the above ground volume of the tree, V_t , and increase with light intensity I , specifically, following a Monod-type function (Huisman & Weissing 1994). Then:

$$P = \frac{vV_t p I}{H + I}, \quad (6)$$

where v , p and H are constant coefficients representing the ratio of the crown volume over the above ground volume, the maximum specific carbon uptake rate (for a unit of crown volume) and the light intensity required for carbon uptake at half the maximum rate, respectively.

Let the respiration rate, R , be an increasing function of the tree's total volume, $V_t + V_s$. We assume here that the respiration rate is proportional to the total volume of the tree such that:

$$R = r(V_t + V_s), \quad (7)$$

where r is a constant coefficient. Then, P and R are both functions of α and l .

Given that a constant fraction, ρ , of the net production is allocated to tree growth, that is $\rho(P-R) = d(V_t + V_s)/dt = [(dV_t/dl) + (\partial V_s/\partial l)](dl/dt)$, the tree growth dynamics in terms of its length are governed by the differential equation:

$$\frac{dl}{dt} = \frac{\rho(P-R)}{\left(\frac{dV_t}{dl} + \frac{\partial V_s}{\partial l} \right)}. \quad (8)$$

The mortality rate of the tree during a unit of time, M , reflects the condition of the net productivity of the tree: the negative net productivity often leads to tree death. The amount of carbohydrate reserves determines the length of period of stress for which the tree can survive (Kozłowski *et al.* 1991). It is reported that the amount of carbohydrate reserves used for the production of chemical defense substances is reflected in the mortality of trees (Waring 1983). Thus, the mortality rate M can be assumed to be a decreasing function of the net production per volume, $(P-R)/(V_t + V_s)$. Here, we assume that:

$$M = \frac{1}{1 + m \left(\frac{P-R}{V_t + V_s} \right)}, \quad (9)$$

where m is a constant coefficient.

The tree length $l(t)$ at time t is determined by solving equation (8) with an initial condition $l(0) = l_0$. The survival probability of the tree throughout its growing stages (i.e. until it reaches maturity) can be evaluated as:

$$S = \exp - \int_0^T M dt, \quad (10)$$

where T represents the terminal point of the growing stage of the tree, that is, the time when the tree reaches the mature crown position z^* . The terminal point T is thus determined as a function of α from the equation, $z^* = h - l(T) (\cos \alpha + \sin \alpha \tan \theta)$, and the mortality rate M is a function of α and $l(t)$; therefore, the survival probability S is determined as a function of α by equation (10).

3. THE RESULTS OF THE MODEL

A numerical analysis of the model shows that on horizontal ground ($\theta = 0$) the tree survival probability S attains its maximum when it has no trunk inclination, while on a slope ($\theta > 0$) there exists an optimal trunk inclination α^* (> 0) that maximizes the tree's survival probability S , and further that the optimum trunk inclination α^* and the maximum tree survival probability $S(\alpha^*)$ both increase with an increase in the slope angle θ (figure 2a).

Assuming that the survival probability of the tree throughout its growing stage is the most crucial fitness component (which is the case if, for instance, the death rate of the tree gets negligibly small once its crown reaches maturity and no significant variation exists in regeneration rate), these points clearly indicate the adaptive significance of trunk inclination on slopes.

An optimal trunk inclination ($\alpha^* > 0$) on a slope ($\theta > 0$) results from the balance between the positive effects (by shortening the distance from the canopy surface, which in turn increases photosynthetic and growth rates and reduces death rate), and the negative effects (by adding the cost of supporting organs, which in turn increases respiration and death rates and reduces growth rate), which are dynamically varied through the growth process, on the tree's survival that a range ($0 \leq \alpha < \theta$) of trunk inclination brings about. (This is because, with an increase in α , the positive effect (benefit) of trunk inclination increases in the range, $-(90^\circ - \theta) \leq \alpha \leq \theta$, and decreases thereafter, while the negative effect (cost) decreases in the range, $-(90^\circ - \theta) \leq \alpha \leq 0^\circ$, and increases thereafter up to 90° , so an optimal trunk inclination should exist on a slope ($\theta > 0$), and must be downward ($\alpha^* > 0$) and less than the slope angle ($\alpha^* < \theta$).)

Given a slope angle $\theta (> 0)$, under poorer light conditions (i.e. under a lower light intensity, I_0), although the maximum tree survival probability, $S(\alpha^*)$, is lower, the improvement of the tree survival probability S by trunk inclination, measured by $S(\alpha^*)/S(0)$, is greater (figure 2b). Further, under a lower light intensity, the increase in the maximum tree survival probability with an increase in the slope angle θ is greater (figure 2b); the significance of this fact

Figure 2. The results of numerical analysis of the model. (a) The effect of the slope angle θ on the tree survival probability $S(\alpha)$. The curves from the bottom represent the functions $S(\alpha)$ for $\theta = 0^\circ, 10^\circ, 20^\circ, 30^\circ, 40^\circ$ and 50° , respectively, with other parameters fixed ($I_0 = 1.5$, $h = 15$, $\kappa = 0.17$, $D = 0.6$, $c = 0.01$, $\rho = 0.1$, $v = 4$, $p = 5000$, $H = 1.0$, $r = 1000$, $m = 0.9$, $z^* = 5$, and $l_0 = 0.1$). The symbol '○' on each line represents the point $(\alpha^*, S(\alpha^*))$, where α^* is the trunk inclination α that maximizes $S(\alpha)$. (b) The effect of θ and the light intensity at the canopy, I_0 , on $S(\alpha)$. The two bundles of curves represent the two sets of functions $S(\alpha)$, $\theta = 0^\circ, 10^\circ, 20^\circ, 30^\circ, 40^\circ$ and 50° (from the bottom) for $I_0 = 1.2$ (the lower bundle, thick) and 1.5 (the upper bundle, thin), where the other parameters take the same values as in (a). The symbols '○' and '●' on each of the curves represent the point $(\alpha^*, S(\alpha^*))$. (c) The effect of θ and shade tolerance $1/H$ on $S(\alpha)$. $1/H = 1.67$ (the higher bundle, thick), 1.25 (the middle bundle, thin), and 1.0 (the lower bundle, broken). (d) The effect of θ and the light extinction rate κ on $S(\alpha)$. $\kappa = 0.13$, (the upper bundle, thick), 0.15 (the middle bundle, thin) and 0.17 (the lower bundle, broken). In (c) and (d), each bundle is composed of curves representing the two sets of functions $S(\alpha)$, $\theta = 20^\circ$ (lower) and 40° (higher). Here '○' and '●' represent the points $(\alpha^*, S(\alpha^*))$ of the same slope angles. Comparisons of '○' or '●' show the tendency for the optimum angle of trunk inclination α^* to get greater either when the shade tolerance $1/H$ gets smaller, or when the light extinction rate κ increases.

would be clearer if we imagine that the opposite trend were the case, in which tree survival under a low light intensity would remain hopelessly low even on steeper slopes.

For the effects of the light extinction coefficient κ and the effects of the shade tolerance of the tree $1/H$, we have similar but slightly modified results to those of the lower light intensity, I_0 : (i) The maximum survival probability, $S(\alpha^*)$, is greater, while the optimum trunk inclination α^* is smaller for trees with greater shade tolerance $1/H$ (figure 2c); (ii) the effect of trunk

inclination on the survival of the tree, measured by $S(\alpha^*)/S(0)$, is greater for trees with lower shade tolerance $1/H$ (figure 2c); (iii) as the light extinction coefficient κ decreases (i.e. the light supply conditions improve), the maximum survival probability $S(\alpha^*)$ increases, whereas the optimum trunk inclination α^* decreases (figure 2d); and (iv) as the light extinction coefficient κ increases (i.e. the light supply conditions worsen), the effect of trunk inclination on the survival of the tree, measured by $S(\alpha^*)/S(0)$, increases (figure 2d).

Figure 3. Data on the relationship between trunk inclination and slope angle obtained from a field study. Two under storey species *R. tashiroi* (Rt) and *E. japonica* (Ej), and the dominant canopy species *D. racemosum* (Dr) in Q1 are featured. A positive correlation is detected with significant regression only with Rt ($p = 0.0053$), while no significant relationship is found with Ej ($p = 0.5904$) or Dr ($p = 0.3603$). Here, the variance in trunk inclination increases with the slope of the subplots.

4. TESTING THE MODEL'S PREDICTIONS

We tested the model's predictions against the data obtained by one of us (R.I.) from a field study in

warm-temperate evergreen forests on a southern island of Japan, Yakushima ($30^{\circ} 20' \text{ N}$, $130^{\circ} 50' \text{ E}$), where an under storey species, *Rhododendron tashiroi*, exists under the dominant canopy species, *Distylium racemosum*. The field study was conducted in two quasi-rectangular permanent plots, Q1 and Q2, established in 1983 (Kohyama *et al.* 1984). Both of them are located in the south-western part of Yakushima. The plot Q1 (altitude: 700 m; S 27° –W; $70 \text{ m} \times 60 \text{ m}$) is situated on a slope extending under a ridge, while plot Q2 (altitude: 540 m; N 25° –W; $70 \text{ m} \times 70 \text{ m}$) is on a slope within a valley. The value of κ was observed to be 0.16 in both plots, and the I_0 value at Q2 was estimated to be about 84% of that at Q1, on average.

First, the data on the under storey species *R. tashiroi* show increases both in trunk inclination (figure 3a) and tree density (the upper left graph of figure 4b) with an increase in the slope angle, supporting the first main model prediction indicated in figure 2a. Figure 3a also shows that an increase in the variance of trunk inclination occurs with an increase in the slope angle; this can be explained by the model, which suggests that trees with a greater range of trunk inclination may survive on a steeper slope (see figure 2a, where imagining a horizontal line that represents a level of survivorship, would elucidate the range of trunk inclination required for that level of survivorship with each slope angle).

Secondly, on comparing the data of the under storey species from the plots (see the top graphs of figure 4b), a sharper increase in tree density against the slope angle is detected in the plot with a lower light intensity Q2, where the under storey species can exist only on very steep areas. This result supports the model's prediction indicated in figure 2b that under a lower light intensity, I_0 , the increase in the maximum tree survival probability, $S(\alpha^*)$, with an increase in the slope angle, θ , is greater.

Thirdly, in a census of saplings, it was found that *R. tashiroi* regenerated more poorly under the closed canopy than the sympatric under storey species *Eurya japonica*, suggesting that the under storey species, *R. tashiroi*, is less shade tolerant than *E. japonica*. Comparison between figures 3a and 3b thus supports the model's prediction indicated in figure 2c that species which are less shade tolerant should exhibit greater trunk inclination on slopes. Also, comparison between the top right and middle graphs in figure 4b, which indicates that the distribution of *R. tashiroi* tends to be confined to steeper slopes compared with *E. japonica*, supports another of the model's prediction, indicated in figure 2c, that a greater increase in the maximum tree survival probability, $S(\alpha^*)$, with an increase in the slope angle θ is observed for species of less shade tolerance.

To examine the effect of light extinction rate, it is necessary to compare forests of different light extinction rate and to observe a general tendency in the trunk inclination and density of under storey species. Yoda (1971) reported that the average light extinction rates per leaf area index (LAI), k , varies widely among forests of different types: for example, the ratio k_a/k_e takes values between about 0.6–0.8, where k_a and k_e

Figure 4. Data on tree density and slope angle. (a) The spatial distribution of sufficiently large trees (with D.B.H. over 4 cm) of the under storey species, *R. tashiroi*, over the slope plots Q1 and Q2. The bars are scaled to indicate relatively local tree density. (b) Data on the relationship between tree density and slope angle for trees (with D.B.H. over 4 cm) of the under storey species (upper graphs), and for mature trees (with D.B.H. over 10 cm) of the dominant canopy species, *D. racemosum*, (lower graphs) found in the site Q1 (left graphs) and Q2 (right graphs), respectively. A positive correlation is detected with significant regression ($p = 0.0419$ for Q1 and $p < 0.0001$ for Q2) for the under storey species, while regression is not significant ($p = 0.09174$ for Q1 and $p = 0.5137$ for Q2) for the canopy species.

represent the values of k for deciduous forests and evergreen forests, respectively. This difference in light extinction rate is large enough to cause a significant difference in the degree of trunk inclination. The model results shown in figure 2d therefore predict that a greater degree of trunk inclination and a greater increase in tree density with an increase in the slope angle should be observed in evergreen forests of thick-leaved species rather than in deciduous forests. Testing this prediction requires an extensive field survey, beyond the scope of the present study, that allows a systematic comparison between under storey trees sharing similar ecological properties in evergreen and

deciduous forests under similar environmental conditions except for their light extinction rates.

Noting that the canopy species, whose trunks do not incline (figure 3b) because of a drastic increase in the cost of supporting organs once tree height exceeds a critical level (Ishii, *in preparation*), exhibit no correlation between tree density and slope angle, no factor that correlates with slope angle is responsible for the biased distribution of the under storey species towards steeper areas on the slopes. It thus seems reasonable to conclude that the under storey species, *Rhododendron tashiroi*, is able to sustain its population under the dominant canopy species by enhancing tree survival

with optimal trunk inclination on slopes, while the other sympatric under storey species *E. japonica*, coexists with the canopy species by enhancing reproductive effort (Kohyama 1992; Aiba & Kohyama 1996).

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REFERENCES

- Aiba, S. & Kohyama, T. 1996 Tree species stratification in relation to allometry and demography in a warm temperate rain forest. *J. Ecol.* **84**, 207–218.
- Del Tredici, P. 1992 Natural regeneration of *Ginkgo biloba* from downward growing cotyledonary buds (Basal Chichi). *Am. J. of Bot.* **79**, 522–530.
- Huisman, J. & Weissing, F. J. 1994 Light-limited growth and competition for light in well mixed aquatic environments: an elementary model. *Ecology* **75**, 507–520.
- King, D. 1981 Tree dimensions: Maximizing the rate of height growth in dense stands. *Oecologia* **51**, 351–356.
- Kohyama, T. 1992 Size-structured multi-species model of rain forest trees. *Funct. Ecol.* **6**, 206–212.
- Kohyama, T., Sakamoto, K., Kobayashi, T. & Watainabe, R. 1984 Structure of tree community of a primary lucidophyll forest in the Koyohji basin. In *Conservation reports of the Yakushima wilderness area, Kyushu, Japan* (ed. M. Numata (in Japanese)), pp. 375–397. Tokyo: Environment Agency of Japan.
- Kozlowski, T. T., Kramer, P. J. & Pallardy, S. G. 1991 *The physiological ecology of woody plants*. London: Academic Press, Inc.
- Mattheck, C. 1991 *Trees – The Mechanical Design*. Heidelberg and New York: Springer Verlag.
- Nakai, T. & Yamai, R. 1982 Properties of the important Japanese woods – the mechanical properties of 35 important Japanese woods. *Bull. Forestry and Forest Products Res. Inst.* (in Japanese), **319**, 13–46.
- Putz, F. E., Coley, P. D., Lu, K., Montalvo, A. & Aiello, A. 1983 Uprooting and swapping of trees: structural determinants and ecological consequences. *Can. J. For. Res.* **13**, 1011–1020.
- Sakai, A. Ohsawa, T. & Ohsawa, M. 1995 Adaptive significance of sprouting of *Euptelea polyandra*, a deciduous tree growing on steep slopes with shallow soil. *J. Plant Res.* **108**, 377–386.
- Shimada, K. 1994 Topographical distribution of five pioneer species and significance of their tree form in natural forests on Mt Takao. *Jap. J. Ecol.* **44**, 293–304.
- Umeki, K. 1995 Modeling the relationship between the asymmetry in crown display and local environment. *Ecol. Model.* **82**, 11–20.
- Waring, R. H. 1983 Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res.* **13**, 327–354.
- Yoda, K. 1971 *Forest ecology* (in Japanese). Tokyo: Tsukiji shokan.

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