The adaptive significance of trunk inclination: a further thought

Reiichiro Ishii and Masahiko Higashi

Center for Ecological Research, Kyoto University, Kyoto 606, Japan

A recent paper in this journal has criticized our previous study, in which we identified an adaptive significance of trunk inclination on slopes. Our main argument was that a tree on a slope may gain some benefit by leaning, which provides the tree with shorter access to the canopy light, and thus a better chance for survival, and that if this benefit outweighs the cost involved in leaning, trunk inclination will be favoured by selection. Although the criticisms are based on some misunderstandings, the situations considered in the critique, which are different from ours, have inspired us into an extension of our previous study. In the course of a reply to the criticisms, we present a further thought on the adaptive significance of trunk inclination in a broader scope. Specifically, we show that our model, with its modified formulation of the benefit component of tree leaning, may evaluate the fitness of a tree with its trunk inclined. It can also be used to examine the conditions for tree leaning, and make predictions on the optimal tree leaning in any situations, including canopy gaps and permanent openings, which the critique is mainly concerned with.

Keywords: trunk inclination; supporting wood; cost estimation

1. INTRODUCTION

Loehle (1997) has criticized our recent study (Ishii & Higashi 1997), in which we identified an adaptive significance of trunk inclination on slopes. Our main argument was that a tree on a slope may gain some benefit by leaning, which provides the tree with shorter access to the canopy light, and thus a better chance for survival, and that if this benefit outweighs the cost involved in leaning, trunk inclination is favoured by selection. Although Loehle's (1997) criticisms are based on some misunderstandings of our model, the situations that he considers, which are different from the one that we dealt with, have inspired us to try an extension of our previous study. The aim of this note is, therefore, to present, in the course of a reply to Loehle's (1997) criticisms, a further thought on the adaptive significance of trunk inclination in a broader scope.

We first note that Loehle (1997) bases some of his arguments on an erroneous assumption that we 'used an optimality argument to predict how much a tree should respond to sidelight'; we never dealt with the response to sidelight, nor, thus, situations involving sidelight, such as canopy gaps and permanent openings (e.g. river margins), which he specifically considers. One of his claimed flaws in our model is that 'the ephemeral nature of most gaps was ignored'. This is an example of the arguments that are based on an erroneous assumption of our model, and is thus irrelevant.

Loehle (1997) claims the following three problems in our estimation of leaning cost: (i) the estimation of crown mass, (ii) the absence of elasticity, and (iii) the cost estimation of supporting. We discuss these points in response to his criticisms.

2. THE ESTIMATION OF CROWN MASS

Loehle (1997) states that our assumption of crown mass being proportional to trunk mass is not correct, by referring to the field study of Strauss & Ledig (1985), which deals with several conifer species (in the genus *Pinus*). In their study, the allometric coefficient (b value) of the trunk–foliage relationship takes considerably varied values (from 0.54 to 1.02) depending on the species, even if they are within the same genus. On the other hand, King (1981), for example, shows the appropriateness of assuming a constant ratio of crown weight to trunk weight with his field data of a broad-leaved species (*Populus tremuloides*), the ratio of which does not change significantly throughout its trunk growth. Therefore, the assumption of our theoretical model seems quite reasonable for application to broad-leaved species, which is the case in our study.

As the ratio of crown weight to trunk weight varies in a broad range (including value $b = 1$) depending on the tree species, it will be an interesting extension of our study to incorporate a trunk–foliage allometric coefficient and examine its effect.

3. TRUNK ELASTICITY

Loehle (1997) claims that trunk elasticity plays a significant role in reducing the leaning cost of small trees and not of large trees. Further, referring as extreme examples to bamboo and *Rhododendron* species, he stresses that, in general, small species have elastic wood and that this is the very reason that trunk inclination is seen in small species and not in large species. Elastic stability, however, exists in trees of any size. MacMahon (1973) revealed that

elastic stability requires the diameter of a tree to be the length of the tree to the power of $3/2$ (the exponent takes different values with different assumptions of wood traits; MacMahon & Kronauer 1976), but the critical size to distinguish size-dependent risk structure, which Loehle claims, is not known. The argument by Loehle that small species have more elastic wood seems doubtful. We could not find such a tendency in the list of Young's modules of elasticity measured for 142 tree species, including seven understory species, some of which belong to the same families as our samples, Ericaceae and Theaceae (Kishima *et al.* 1962; Nakai & Yamai 1982).

Therefore, it is rather subtle that the difference in leaning cost among different sizes of trees is due to differences in elasticity, and that this difference is more clearly due to that in size itself (or its proportional weight, which causes differential bending forces). In our model, we assume that trees have enough strength to almost withstand the constant bending moment generated by their own weight when they lean. This seems to be the case for most tree species and certainly for the tree species observed in our field study. In the case of those species, trees can have enough room to endure the temporal bending moment added by an external force such as a wind.

Moreover, bamboo is not a good example to represent general small tree species, because it has quite unique properties which contribute to its outstanding elasticity; the pith cavity and parallel fibres are extremely well arranged in the longitudinal direction. On the other hand, it lacks the secondary thickening growth (Shimachi *et al.* 1985) of trunks. In dicotyledon or gymnosperm species of trees, the pith cavity and parallel fibres do not exist, while secondary thickening growth is commonly seen to characterize the thickening growth pattern of their trunks (Shimachi *et al.* 1985).

4. THE COST ESTIMATION OF SUPPORTING WOOD

As the most serious flaw in our model, Loehle (1997) claims that we failed to consider the cost of tree leaning in slowing down tree growth by diverting photosynthetic production to the supporting organ. In fact, our model does incorporate this cost (expressed in equation (8) in Ishii & Higashi (1997)), as well as the respiration cost. Thus, this criticism is invalid.

As for the respiration cost, it is a possible alternative to assume that the respiration rate is proportional to the surface of the trunk (i.e. the second power of trunk length), though there is not enough experimental evidence to decide this factor. For example, from the field study by Gerrish (1990), who reported on the relation between the volumes of the living part (inner bark) and the whole trunk of a tree species, we can estimate the exponents of inner bark volume against trunk length to be about 2.59 on average, with a considerable variance. With such varied values, our simplification that the factor is 3 is not less adequate than to simplify it to 2, as Loehle suggests.

From these arguments, we conclude that Loehle's (1997) claim that our 'calculations of the costs of leaning are flawed' is invalid. Our model derived a prediction of the dependence of the optimal trunk inclination on three parameters, the shade tolerance of tree species, the light

extinction rate in a forest, and the light intensity at the canopy surface of the forest. Specifically, the prediction suggests the tendency that species with higher shade tolerance should have less trunk inclination than those with less shade tolerance, and we pointed out that this prediction was consistent with the data of the two understory species, *Rhododendron tashiroi* and *Eurya japonica*, observed in our field study. Loehle (1997) dismissed this case merely as an exception, claiming that many small shade-tolerant species lean. He seemed to miss the point that such a tendency can be tested only by comparing species among which no significant difference exists in traits other than the one concerned (i.e. shade tolerance in this case). The two understory species in our field study, observed in the same site, are likely satisfy this necessary condition, while the species that he listed may not. It should be noted that there may be more than one factor responsible for a single phenomenon. We might observe a more shade-tolerant species 'A' leaning more than a less shade-tolerant species 'B' if some of the differences in other environmental factors favour it. The possible prediction from our study (Ishii & Higashi 1997) is that the forest where species A is observed (i) has more dense foliage, (ii) has less light intensity at the canopy surface, or (iii) has a steeper slope, than the forest where B is observed.

Although we, of course, recognize the importance of the reproductive component of fitness, in our previous study (Ishii & Higashi 1997) we specifically focused on the situation where the survival probability of the tree throughout its growing stage is the most crucial fitness component. This is the case if the death rate of the tree becomes negligibly small once its crown reaches maturity and no significant variation exists in regeneration rate, as stated in our paper. In more general cases it is necessary to make an estimation of the reproductive component of fitness. Although Loehle (1997) tried to evaluate in terms of a model the reproductive cost dependent on trunk inclination, the model is not valid on slopes. The cost of trunk leaning that Loehle (1997) is concerned with is the disadvantage in reproduction in terms of the reduction of seed dispersal area due to a lowered position for seed scattering of matured trees. On slopes, however, crown position is not always lowered by trunk inclination, as illustrated in figure 1. Crown height from the ground is expressed as $h = l (\cos\alpha + \sin\alpha \tan\theta)$, where l , α and θ are trunk length, trunk leaning angle and slope angle, respectively. With a given slope angle θ , h takes the maximum value when the leaning angle is θ (i.e. $\alpha = \theta$). Therefore, h is a monotone decreasing function α within the range of $0 < \alpha < \pi/2$ and, thus, represents a cost of trunk inclination only in the case $\theta = 0$, that is, in the case of plane sites (figure 1 *a*). The vertical distance between the ground and the tree crown h , which Loehle uses as an indicator of trunk leaning cost, depends not only on trunk inclination but also on the steepness of the slope and, thus, the model result cannot detect the effect of trunk inclination *per se*.

Loehle (1997) appears to agree with our point that tree leaning on slopes should bring a benefit (slope effect), while we agree with his point that tree leaning in situations with sidelight should bring a benefit (sidelight effect), though how he evaluates the tree leaning benefit in those

Figure 1. Illustration showing the effect of trunk inclination on crown height from the ground, h , indicated by lines with arrows on both sides. The bars with black circles represent trunks with crowns. They have the same length l and three different leaning angles; A represents vertical position, $\alpha = 0$. In (a), where the steepness of the ground θ is 0 (i.e. no slope), the crown height h is a monotone decreasing function of leaning angle α ($0 < \alpha < \pi/2$). In (b) where the ground has a slope $\theta > 0$, the crown height h attains a maximum value when the trunk leaning angle α equals the angle of the slope, θ (position B). Therefore, h is not a monotone decreasing function of α in the range of $0 < \alpha < \pi/2$.

situations is not expressed in his mathematical formulations. The point of content lies in the evaluation of the cost component of tree leaning. As we have above reconfirmed through responding to his criticisms, our model (Ishii & Higashi 1997) can make an appropriate and explicit evaluation of the cost of tree leaning, which is independent of the slope situation, and thus can be applied to any situations, including canopy gaps and permanent openings (e.g. forest edges), which Loehle (1997) is mainly concerned with. This means that our model, with its modified formulation of the benefit component of tree leaning, may evaluate the fitness of a tree with its trunk inclined, and can be used to examine the conditions for tree leaning and make predictions on the optimal tree leaning for any of these different situations.

We thank Dr H. Tabata for his useful comments on botanical knowledge. R.I. is a JSPS research fellow.

REFERENCES

- Gerrish, G. 1990 Relating carbon allocation patterns to tree senescence in *Metrosideros* forests. *Ecology* **71**, 1176–1184.
- Ishii, R. & Higashi, M. 1997 Tree coexistence on a slope: an adaptive significance of trunk inclination. *Proc. R. Soc. Lond. B* **264**, 133–140.
- King, D. A. 1981 Tree dimensions: maximizing the rate of height growth in dense stands. *Oecologia* **51**, 351–356.
- Kishima, T., Okamoto, S. & Hayashi, S. 1962 *Atlas of wood in colour*. Osaka, Japan: Hoikusha.
- Loehle, C. 1997 The adaptive significance of trunk inclination on slopes: a commentary. *Proc. R. Soc. Lond. B* **264**, 1371–1374.
- MacMahon, T. A. 1973 Size and shape in biology. *Science* **179**, 1201–1204.
- MacMahon, T. A. & Kronauer, R. E. 1976 Tree structures: deducing the principle of mechanical design. *J. Theor. Biol.* **59**, 443–466.
- Nakai, T. & Yamai, R. 1982 Properties of the important Japanese woods—the mechanical properties of 35 important Japanese woods. *Bull. Forestry Forest Prod. Res. Inst.* **319**, 13–46.
- Shimachi, K., Saeki, H., Harada, H., Shiokura, T., Ishida, S., Shigematsu, Y. & Sudo, S. 1985 *Wood science*. Tokyo: Buneido.
- Strauss, S. H. & Ledig, F. T. 1985 Seedling architecture and life history evolution in pines. *Am. Nat.* **125**, 702–715.