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BRIEF COMMUNICATION

A latitudinal cline in leaf inclination of *Dryas octopetala* and implications for maximization of whole plant photosynthesis

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Abstract

Mean leaf inclination of the arctic and alpine shrub *Dryas octopetala* is a function of latitude and this functional relationship is consistent with a model that maximizes photosynthesis of the total plant canopy.

Additional key words: leaf angle; plant modeling.

Dryas octopetala is a dwarf shrub with a circumpolar distribution in the Arctic and a range from more than 80°N latitude to 35–45°N in Colorado, Bulgaria, Japan, and the Russian Caucasus (Hulten 1968, Polunin 1980, Ohwi 1984). Previously, this author has taken advantage of the wide latitudinal distribution of this species to compare leaf inclination angles of *D. octopetala* near Longyearbyen, Svalbard with those from Obersdorf, Germany (Herbert 1993). This comparison indicated that leaves were less inclined towards the vertical in the Svalbard population than in the population at the more southern latitude. This communication reports additional measurements, including data from 12 different geographical regions in Europe and North. Furthermore, this study shows that the observed relationship between leaf angle and latitude is consistent with a model that maximizes total plant photosynthesis.

Mean leaf inclination angles were measured for populations of *D. octopetala* at twelve sites ranging from polar to alpine areas in North America and Europe. Measurements were limited to unshaded sites on a horizontal substrate. All leaves in the chosen study area were measured, except for those that were damaged or immature. A small plastic dial inclinometer was used to measure the inclination of the steepest line in the plane of the leaf (Herbert 1983, 1993). For leaves in each population, corresponding to a particular geographical location, the circular mean inclination angle and the parametric circular standard error of the mean (Fisher 1993) were calculated. The periodic characteristic of angular variables suggests that the most precise measure of mean and dispersion of such variables considers angles as vectors. Fisher (1993) and others have developed circular analogs of conventional measures of mean and standard error and it is these measures that are used.

Mean inclination angle of *D. octopetala* decreased as latitude increased (Fig. 1). Median inclination angles were calculated and show a similar relationship. A linear regression line is shown as a guide but should not be used to imply anything about the nature of the dependence of leaf angle on latitude.

Inclination angles and positions of plant leaves are particularly important for maximization of photon interception and photosynthesis when solar photon flux is low and for protection from heat stress and water loss when solar flux is high (Kuroiwa 1970, 1978, Herbert 1991). Herbert and Nilson have described models of photon interception and total plant canopy photosynthesis by an array of leaves vertically stacked and irradiated from above by the direct solar beams (Nilson 1968, Herbert 1989, Herbert and Nilson 1991). Fig. 2*A* shows the result of a simulation using a two-dimensional model described by Herbert and Nilson (1991). This model predicts that upper canopy leaves will be oriented at an acute angle with respect to the solar beam when total plant canopy photosynthesis is maximized. Furthermore, the set of leaf angles that maximizes photosynthetic rate is identical to the set of leaf angles that minimizes the between leaf

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variance in photosynthetic rate (Herbert and Nilson 1991). The maximization model of Herbert and Nilson (1991) assumes that the relationship between photosynthetic rate and incident flux is described by the Michaelis-Menten function (rectangular hyperbola). For the results of computations shown in the present study, parameters in the Michaelis-Menten function are set so that that the photosynthetic rate of a leaf surface perpendicular to the solar beam is 75 % of maximum. All incident photon flux not absorbed by one of the canopy leaves must be absorbed by the last layer of leaves or the optimization procedure will not converge on a single set of leaf angles (Herbert and Nilson 1991). Therefore, the model includes one large horizontal leaf at the bottom of the canopy in addition to the array of upper canopy leaves.

The present study extends the model of Herbert and Nilson (1991), using a new two-dimensional ray-tracing algorithm written by the author. This algorithm permits total plant canopy photosynthesis to be calculated when the direct solar beam is not on the vertical axis of the plant canopy. Comparison of Fig. 2*A* and *B* shows that the new model predicts that leaf surfaces will be more inclined towards the vertical as solar elevation increases, if total plant canopy photosynthesis is maximized. This prediction is consistent with field observations of *D. octopetala*. Leaf inclination angles of *D. octopetala* are high at low latitudes, where average solar elevation is high.

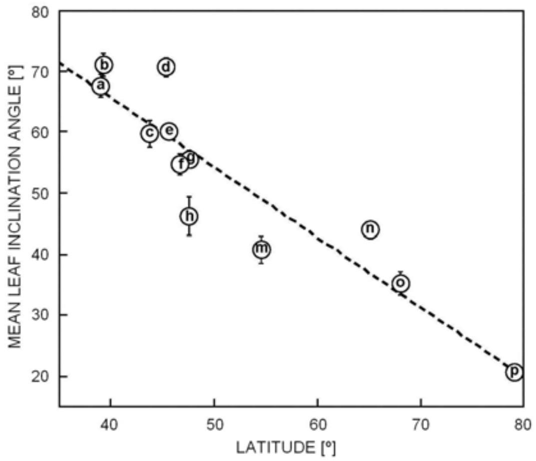

Fig. 1. Mean circular statistical leaf inclination angle *vs.* latitude for *Dryas octopetala*. *Error bars* are circular analogs of standard error of the mean. *The dashed line* represents the best least-squares straight line to mean inclination angle. Labels indicate geographical site, with numbers of measurements at each site indicated: a – Cottonwood Pass, Colorado USA (145); b – Weston Pass, Colorado USA (117); c – Rocky Mountains, Caucasus, Russia (224); d – Vanoise Region, France (119); e – Fagaras Mountains, Romania (591); f – Falzarago Pass, Dolomites, Italy (203); g – Dachstein Mountains, Austria (190); h – Obersdorf, Germany (137); m – Teesdale, England (149); n – Circle Hot Springs, Alaska (288); o – Abisko, Sweden (220); p – Longyearbyen, Svalbard, Norway (167).

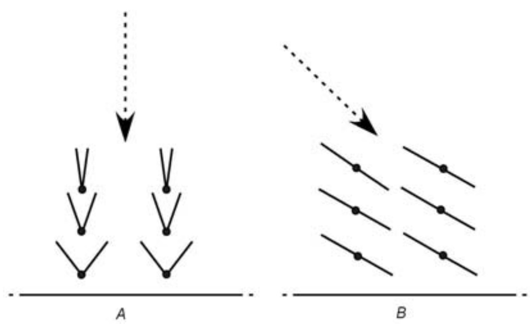

Fig. 2. Orientations of 12 leaf surfaces predicted by a model maximizing total plant photosynthesis. Simulation permits rotation of leaf surfaces about a point indicated by a filled circle. The direct solar beam, indicated by *the dashed arrow*, is elevated at 90° (*A*) or 46° (*B*) above the horizon. The horizontal background leaf is sufficient in length to capture all the incident solar beams passing through the array of 12 leaves.

Maximization of photosynthesis is only one of many factors that might contribute to generation of a latitudinal cline in leaf inclination. Further studies are needed on how other factors, such as temperature, might correlate with leaf inclination. However, the observation of a relationship between leaf inclination and latitude, and a photosynthetic model consistent with that relationship, offer a stimulus and point of departure for future work.

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