Solar Irradiation Increases Floral Development Rates in Afro-alpine *Lobelia telekii*

Amphiscians *n. pl.* [fr. Gr. *amphiskios,* casting a shadow in both directions] The inhabitants of the tropics.

Flowers in arctic and alpine environments exhibit a variety of adaptations to cold. Parabolic flower shape and heliotropism have been shown to increase floral temperatures in arctic and alpine plants (Hocking and Sharplin 1965, Kevan 1975, Smith 1975, Knutson 1981). These authors have suggested that such solar-thermal adaptations may increase floral development rates and facilitate pollination by warmth-seeking insects; however, no relationship between insolation and floral development has yet been demonstrated.

The densely packed flowers around the large cylindrical inflorescences of *Lobelia telekii* on Mount Kenya are fixed with respect to compass direction, providing a natural experiment on the effects of solar irradiation. During a study of *Lobelia* pollination biology (Young 1982), I found a pattern of floral maturity that indicated solar irradiation was associated with significantly increased development rates of flowers and pods. In addition, there was a north to south shift in development rates coincident with the seasonal shift in solar orientation at the equator. This appears to be the first demonstration of any seasonal biological phenomenon in the tropics associated with a shift in solar angle.

Lobelia telekii is a common plant on Mount Kenya at altitudes of 3800 to 4500 m. At reproduction the rosette produces a cylindrical inflorescence up to 3 m tall. The inflorescence is densely packed with protandrous flowers. The terminal inflorescence matures progressively upwards from the base. In 1979 and 1980, a pollination study was carried out on *Lobelia telekii* in the upper Teleki Valley on Mount Kenya (Young 1982). In March 1979, twenty young inflorescences were selected for longterm monitoring as part of this study. All were less than one month old. At one or two heights on each inflorescence, the maturity of marked flowers was recorded at each of four compass directions—60°, 150°, 240°, and 330°. These directions were chosen for convenience; the valley bottom was oriented 30° off of due east-west. The same flowers were surveyed throughout the study period. The reproductive states of the flowers were classed as follows: 1) flower in bud, 2) flower in the male state, 3) flower in the female state, 4) flower no longer receptive but not yet dispersing seeds, 5) pod dispersing seeds, and 6) all seeds dispersed.

The records of developmental state were analyzed for June 1979 (80 flowers) and January 1980 (120 flowers). All flowers in this study were in reproductive states 1, 2 or 3 in the June survey, and in states 4 or 5 in the January survey. Any set of four marked flowers at a given height on an inflorescence that did not differ from each other in their degree of maturity were not included. Floral development in *Lobelia telekii* was very slow, and a given flower would remain in a particular reproductive state for up to several weeks. Therefore even many days difference in floral development may not have resulted in flowers being in different stages at any particular time. Given these slow development rates, the patterns demonstrated below are even more striking.

For each set of four flowers that were not all in the same reproductive state, the flowers that were more mature were recorded by compass direction. There were 12 such sets (out of 20) in the June survey, and 17 such sets (out of 30) in the January survey. For each surveyed compass direction, a vector was calculated with a magnitude equal to the number of sets in which the flowers facing that direction were more mature than at least some of the other marked flowers at the same height on the inflorescence. For example, if the marked flowers facing (approximately) east were in state 3, the flower facing north in state 2, and the flowers facing west and south in state 1 for a given set, then the east and north vectors would each be increased by one. These raw data vectors are shown as dotted lines in Figure 1. Because the surveyed compass directions were 30° off due east, west, north, and south, the magnitudes of new vectors were calculated at 0°, 90°, 180°, and 270°, representing the relative components of the raw data vectors and shown as solid lines in Figure 1. In addition, a single summed vector was calculated for both dates, shown as arrows in Figure 1.

Departure from a uniform distribution in the raw data was examined with a χ^2 test (June, $\chi^2 = 6.80$, df = 3, $P < .10$; January, $\chi^2 = 21.25$, df = 3, $P < .001$). At both dates, the flowers on the east sides of the inflorescences were more mature than the flowers on the west sides of the inflorescences, and the effect had greatly increased by January. There was also a significant north to south shift in relative floral maturity from June to January ($\chi^2 = 5.18$, df = 1, $P < .025$).

Direct insolation in alpine environments is likely to be important because air temperatures are low and irradiation is intense. As in alpine areas elsewhere, mornings are nearly always clear and afternoons usually cloudy in the alpine areas of Mount Kenya and Kilimanjaro (Salt 1954, Hedberg 1964, Allen 1982, and pers. obs.). Therefore east-facing surfaces receive more direct sunlight than west-facing surfaces. Hedberg (1964) reports 'from an ecological point of view this diurnal cycle is of course very important, since the screening of direct sunlight causes a rapid

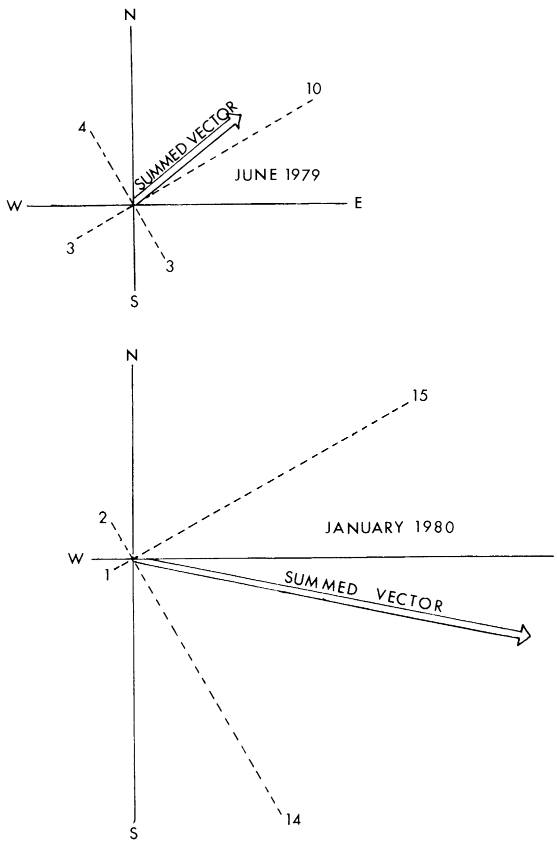

FIGURE 1. Relative maturity of flowers in June 1979 and pods in January 1980. Dotted lines represent raw data; the length of the lines is proportional to the number of times that flowers or pods in a direction were more mature than those facing in at least one other direction (see text). The solid lines represent the north, west, south, and east components of the raw data vectors. The 'summed vectors' are determined from all dotted vectors.

decrease in temperature' (p. 80). The trend for east-facing flowers to be more mature than west-facing flowers increased from June to January. The conditions that favor east-facing flowers were consistent throughout the study, and the effects can be expected to be additive.

Flower buds on very young inflorescences were similarly developed at all compass directions, so the observed differences in relative maturity were due to differential development rates rather than difference in the time of initiation of floral development. The shift in relative floral maturity from north to south and the increased relative maturity of east-facing flowers from June to January also indicate that differential development rates were responsible for differential maturity.

In East Africa, the trade winds shift from the southeast in May to September to the northeast in November to February (Pratt and Gwynne 1977). However on the western side on Mount Kenya at altitudes above 3800 m, the winds are restricted to daily upslope and nightly downslope flow in the direction of west-facing valleys (pers. obs.). The *L. telekii* inflorescences in this study therefore did not experience any north–south shift in prevailing winds.

Mount Kenya lies directly on the equator, so the noonday sun is 23° north of vertical in late June and 23° south of vertical in late December. Mountaineers have long known that the faces of East African mountains usually retain their snow longer when they are oriented away from the sun (Allen 1982); however, no such seasonal north–south fluctuations have previously been shown to affect equatorial plants. In June 1979, the magnitude of the north vector was more than double the magnitude of the south vector. In January 1980, the magnitude of the south vector was 40 percent greater than the magnitude of the north vector. This study demonstrates an effect of a north–south fluctuation on floral development.

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