Microenvironmental Role of a Secreted Aqueous Solution in the Afro-Alpine Plant Lobelia keniensis

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Microenvironmental Role of a Secreted Aqueous Solution in the Afro-Alpine Plant *Lobelia keniensis*[1]

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ABSTRACT

Lobelia keniensis, a giant rosette plant endemic to the alpine zone of Mount Kenya, secretes a solution of water and a mucilaginous substance. This solution forms a reservoir of up to 3 liters between the closely appressed leaf bases of the rosette. Experiments reported here show that rosettes drained of this liquid experienced bud temperatures well below freezing, whereas control rosettes never experienced bud temperatures below freezing. The presence of the reservoir did not affect the rate of leaf warming in the morning. The mucilaginous substance was identified as a pectin, which probably reduces evaporation from the reservoir without lowering the freezing temperature of the water.

THE CLIMATE OF TROPICAL ALPINE AREAS is characterized by generally low temperatures, large and rapid diurnal temperature fluctuations, and occasional drought. Tropical alpine plants display a myriad of physiological, morphological, and "behavioral" adaptations to these stresses, including caulescent and acaulescent giant rosettes, dense pubescence, retension of dead leaves, nyctinasty (Hedberg 1964; Coe 1967; Smith 1974, 1979), and retained water (Krog *et al.* 1979).

L. keniensis is a giant rosette plant endemic to Mount Kenya. Individual plants occur in clones of up to 18 rosettes and may live for many decades (Young 1984). *L. keniensis* plants grow in wet situations from 3400 to 4400 m.

The hollow cylindrical inflorescences of giant *Lobelia* species contain large amounts of a mucilaginous solution. Krog *et al.* (1979) suggest that the role of this solution in *Lobelia telekii* on Mount Kenya is protection against nightly freezing of the inflorescence. A similar solution is found in reserve among the leaves of *L. keniensis* rosettes (Fig. 1). This solution is at least partly secreted by the plant itself and contains a mucilaginous substance (Hedberg 1964, Coe 1967). Unlike the liquid in *Lobelia* inflorescences, the rosette reservoir is exposed directly to the environment. Similar reservoirs are found on other East African mountains in rosettes of *Senecio brassicaformis, Lobelia aberdarica,* and *Lobelia* species most closely related to *L. keniensis.*

It has been suggested that this reservoir provides protection against freezing or drought (Hedberg 1964, Coe 1967). Coe further suggests that the mucilaginous substance is a biological antifreeze. In contrast, Krog *et al.* (1979) suggest that the similar substance found in *Lobelia* inflorescences is a nucleating agent that prevents supercooling. This paper reports the results of an investigation into the microenvironmental role of the secreted aqueous solution in *L. keniensis.* We show that the reservoir prevents freezing of the leaf bud, and that the mucilaginous substance is neither an antifreeze nor a nucleating agent but a pectin that probably protects the reservoir from evaporation.

MATERIALS AND METHODS

This study was carried out in the Teleki Valley on the western side of Mount Kenya at an elevation of 4100 m in November and December 1979. Eight large *L. keniensis* rosettes of similar size, on 8 different clones, were selected. Four of these were drained of their reservoirs, and 4 were used as controls. Thermocouples were placed deep in the leaf bud, on an exposed leaf surface, and in the reservoir (in the control plants; see Fig. 1). Air temperatures were recorded 30 cm above the ground. From 24 to 28 November 1979, temperatures from these thermocouples were recorded throughout the day and night. From 4 to 6 December, more detailed environmental temperature patterns were recorded. Air temperatures were recorded at ground level and at 50 and 100 cm above the ground. Soil temperatures were recorded at depths of 5 and 10 cm. *Lobelia* bud temperatures were not recorded in December.

A sample of the liquid was collected and taken for

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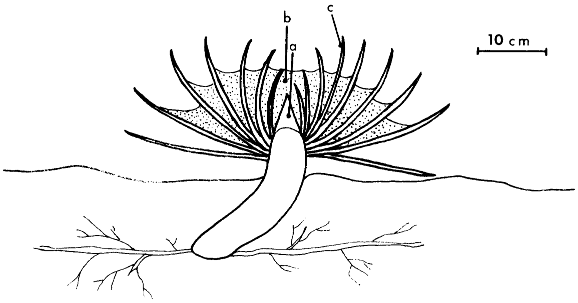

FIGURE 1. Cross section of a *L. keniensis* rosette showing the location of thermocouples: (a) deep in bud, (b) reservoir, (c) leaf surface.

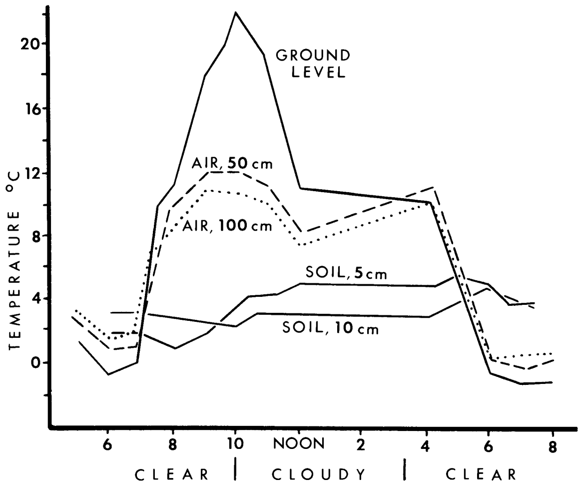

FIGURE 2. Temperature run for 5 December 1979, showing air temperatures at 0, 50, and 100 cm above the ground, and soil temperatures at 5- and 10-cm deep. The soil temperatures represent the means of two values at each depth.

analysis to Dr. Luka Abe, then of the Department of Botany, University of Nairobi.

RESULTS

Rosettes contained up to 3 liters of fluid. It was not possible to remove all of the fluid, and a small amount (< 10 cc) had to be removed daily during the experiment. The minimum nighttime temperatures during the November study period were between −4° and −11°C. Ice formed every night on the reservoirs of the control rosettes: the measured temperature of this fluid never fell below −0.5°C, and the melting point of the ice was measured at 0°C. The minimum bud temperatures for the 4 undrained rosettes were all 0°C. The minimum bud temperatures for 4 drained rosettes were 0°, −3.5°, −6.5°, and −7.0°C (mean, −4.25°; standard error, 1.61°). The buds of drained rosettes experienced significantly lower minimum temperatures over the 4 nights than did the buds of the undrained rosettes ($P < 0.05$).

No significant difference was found between drained and undrained rosettes in the rate at which larger leaves heated up in the morning. Table 1 shows the mean rate of leaf surface heating for control and experimental rosettes during a representative morning (25 November 1979). Although the leaves of drained rosettes warmed somewhat faster than the leaves of undrained rosettes, this difference was not significant. Air temperatures 30 cm above the ground began to increase at the same time as the leaf temperatures (dawn, 7:15–7:30 A.M.), but at a slower rate ($P < 0.001$).

TABLE 1. *The rate of morning heating of the air 30 cm above the ground and of exposed leaves on control and experimental rosettes on 25 November 1979.*

	°C/min	SD	*N*
Leaves on control rosettes	0.35	0.05	4
Leaves on experimental rosettes	0.41	0.13	4
Air 30 cm above the ground	0.13		1

Figure 2 shows a representative daily air and soil temperature range from the December study period. Minimum temperatures were higher in the December period than in the November period, probably because winds disrupted the usual pattern of cold air drainage in the valley bottom. The soil temperature at a depth of 10 cm remained fairly constant throughout the day, 3–4°C. The soil temperature at a 5-cm depth showed a slow daily fluctuation between 1° and 6°C. The soil temperature at 5 cm began to increase much later and increased more slowly than did the air temperature. The night air temperature gradient was clear, ground level air being 2–3°C colder than air 1 m above the ground. During daylight hours, the temperature gradient reversed dramatically.

Dr. Luka Abe identified the mucilaginous substance as a pectin. The *L. keniensis* solution was not ionically active to a measurable degree, confirming the 0°C freezing point.

DISCUSSION

L. keniensis plants experience three major climatic stresses in the alpine zone of Mount Kenya—drought, low minimum temperatures, and large and sudden changes in temperature (Hedberg 1964). The results reported here indicate that the reservoirs present in their rosettes protect the leaf buds from subzero temperatures. These buds contain the sensitive growing meristems. Krog *et al.*

(1979) point out that the high heat of fusion acts to minimize freezing; the high heat capacity of water should also reduce the rate of cooling. In any case, the temperature of the fluid and the buds did not drop significantly below 0°C in the control rosettes.

Leaf temperatures heat up earlier in the morning, and much more quickly, than soil temperatures at the 5-cm depth. This could result in the leaves transpiring before soil moisture was readily available to them—a potentially serious drought stress. Any adaptation that reduced the rate at which leaves warmed in the morning would then be important (Goldberg *et al.* 1984). Experiments have shown that this may be the key to the nightly closing of rosette leaves (nyctinasty) on Mount Kenya; nyctinasty did not affect minimum bud temperatures in Mount Kenya *Lobelia* and *Senecio* species, but did slow down morning leaf heating (A. P. Smith & T. P. Young, pers. comm.). However, the results presented here indicate that the fluid reservoir in *L. keniensis* did not significantly affect the rate at which exposed leaves heat up in the morning.

The pectin in the rosette reservoir did not measurably affect the freezing point of the water, a finding which agrees with the known chemistry of pectins (Whistler & Smart 1953) and with the results of Krog *et al.* (1979) for *L. telekii* inflorescences. In fact, the freezing point depression suggested by Coe (1967) would likely be detrimental in that, by lowering the reservoir temperature required for ice formation, depression of the freezing point would lower the minimum temperature experienced by the buds.

Krog *et al.* (1979) suggested that the mucilaginous substance in the similar fluid in *L. telekii* inflorescences serves as a biological nucleating agent that prevents supercooling. However, supercooling is unlikely except in small, relatively motionless capillaries, and exceedingly rare in higher plants (Levitt 1972). It is almost certain that the large reservoirs of water in *L. telekii* inflorescences and *L. keniensis* rosettes would not supercool even if the plants did not produce pectin or other nucleating agents.

Pectins are strong hydrating agents that protect plants from desiccation (Whistler & Smart 1953). I hypothesize that the pectin in *L. keniensis* rosette reservoirs reduces evaporation rates, especially during drought when reservoir levels drop and pectin concentrations increase. Alan Smith (pers. comm.) further suggests that the mucilage may reduce convection in the reservoir. This would increase the rate at which the ice layer is formed while maintaining relatively higher temperatures in the lower part of the reservoir near the bud.

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LITERATURE CITED

Coe, M. J. 1967. The ecology of the alpine zone of Mount Kenya. Dr. W. Junk Publishers, The Hague.

Goldberg, G. O., F. C. Meinzer, and M. Monasterio. 1984. The role of capacitance in the water balance of Andean rosette species. Plant, Cell and Environment 7: 179–186.

Hedberg, O. 1964. Features of afroalpine plant ecology. Acta Phytogeogr. Suec. 49: 1–144.

Krog, J. O., K. E. Zachariassen, B. Larson, and O. Smidsrod. 1979. Thermal buffering in Afro-Alpine plants due to nucleating agent-induced water freezing. Nature (London) 282: 300–301.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York.

Smith, A. P. 1974. Bud temperatures in relation to nyctinastic leaf movement in an Andean giant rosette plant. Biotropica 6: 263–266.

———. 1979. The function of dead leaves in *Espeletia schultzii* (Compositae), an Andean giant rosette species. Biotropica 11: 43–47.

Whistler, R. L., and C. L. Smart. 1953. Polysaccharide chemistry. Academic Press, New York.

Young, T. P. 1984. Comparative demography of semelparous *Lobelia telekii* and iteroparous *Lobelia keniensis* on Mount Kenya. J. Ecol. 68: 637–650.