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NUTRIENT INPUT TO AN ALPINE TUNDRA: AN AEOLIAN INSECT COMPONENT

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ABSTRACT—Large quantities of non-alpine insects are blown episodically onto some alpine tundras. These events may have return intervals as short as 3 years in Colorado. Windblown depositions of a moth (*Loxstege cerareoles,* Pyralidae) from one episodic event were analyzed to determine the possible influx of soluble nutrients to the alpine tundra. Ten chemicals were identified in or on the insect bodies. Significant external additions of soluble phosphorus and potassium occurred to the alpine, but additions of soluble nitrogen were probably not significant. Phosphorus additions may represent a relatively new input source emanating from contamination by fertilizers used on alfalfa crops on the Great Plains. Potassium inputs may originate in the soils of the Great Plains and may increase buffering capacity in the poorly buffered tundra soils of the Colorado Front Range.

The deposition of windblown insects is an important ecological process in high alpine regions (Swan, 1967; Mani, 1968; Edwards, 1987) with the "aeolian zone" defined as that area of the very high alpine, above the limit of vascular plants, where organisms are primarily or exclusively dependent on nutrients imported by the wind (Swan, 1963, 1967). In these areas, with limited or no primary production, imported nutrients are important. However, in alpine tundra areas, below the aeolian zone but above treeline, the importance of this insect nutrient source is less well understood. Spaulding (1979) estimated carbon input to the aeolian zone in California, and estimates of nitrogen and carbon inputs are available from the Arctic (Edwards, 1972; Edwards and Banko, 1976).

Windblown insects from non-alpine regions occur on Niwot Ridge, Front Range, Colorado (Alexander, 1950, 1951; May, 1980) as a result of two influx processes. The first type is the frequent arrival of non-alpine insects blown by strong upslope summer winds originating on the Great Plains east of the Rocky Mountains (Wellington, 1945). These frequent events bring live insects of many different taxa ranging in size from small flies to large grasshoppers and dragonflies. The second type occurs episodically, when large quantities of a single species of insect are blown onto the Ridge. Single-species influxes may be composed of insects from unusual population highs or from dispersing swarms, i.e., migrating locusts, blown off course. Episodic events differ from frequent influxes by being composed of large numbers of a single species. The frequency of episodic events is difficult to ascertain. Since 1979, we have observed three episodic influxes to Niwot Ridge, indicating a possible short-return interval. However, the last episodic event was in 1985. Grasshoppers frozen in glacial ice in Montana and Wyoming indicate that insect influxes are a long-term phenomenon dating back at least 600 years (Gurney, 1953).

The role of windblown insects in the nutrient balance of alpine tundra is not known, nor are data available to indicate the amount of nutrients that insects may add to an alpine ecosystem. If the alpine tundra is functioning with nutrient deficiencies of nitrogen, phosphorus, and potassium (Faust and Nimios, 1968; May, 1976; Irwin, 1982; Shulls and Mancinelli, 1982), then additions from wind-imported insects may be ecologically significant. Also one chemical of interest in the alpine (DDT, dichloro-diphenyl-trichloroethane) may have a wind-transported origin. Chemical analyses of ptarmigan chicks and their eggs conducted during the International Biological Programme (IBP) identified insects as vectors in the transport of DDT from the plains to the alpine regions on Niwot Ridge (J. D. Ives, pers. comm.). Episodic influxes of insects may transport significant contributions of nutrients or other chemicals, but amounts are hard to quantify because of the temporal rarity of the inputs.

Large outbreaks of the moth *Loxostege cerareolis* (Pyralidae) occurred on the plains of Colorado in May 1985. These moths are the adult stage of the alfalfa web worm, which infests alfalfa crops on the plains.

During population explosions, the moth *L. cerareolis* shifts to a dispersal behavior, often flying at high altitudes (U. Lanham, pers. comm.). Once airborne, dispersal aggregations may be controlled by the powerful Colorado winds which carry them to the high mountains. As live insects encounter the cold alpine air, they tend to fold their wings and fall to the ground (Furniss and Furniss, 1972; Elias, 1982). By June 1985, the episodic moth fallout was apparent on alpine snowfields. We report, here, on the depositional density of moths on Niwot Ridge, following the outbreak in May 1985, and provide minimum estimates of soluble nutrient input to the alpine ecosystem from this episodic event.

MATERIALS AND METHODS—The Saddle study site (3,525 m above sea level) was located on Niwot Ridge, Colorado Front Range, 50 km west northwest of Boulder. The ecological background of this area was summarized by Halfpenny (1982) and Ives (1980).

A permanently marked grid, the Saddle Grid, stretched 550 by 350 m from West Knoll across the Saddle to East Knoll. Six plant communities formed a topoclimatic gradient from the east end of the grid to the west end of the grid: fellfield, dry meadow, moist meadow, shrub tundra, wet meadow, snowbed (May and Webber, 1982). The east end of the transect blew free of snow in the winter and was relatively dry, while the west end was in the snow depositional zone and could be covered by up to 7 m of snow.

On 5 June 1985, we collected moths on the snowfield of the east-facing slop of West Knoll. Collections were made on the snowfield because moths were highly visible on the snow surface. However, moth deposition was also noted on bare ground and in the snow-free plant communities. Samples were taken at 10-m intervals starting at grid marker number 35 on the Saddle Grid and proceeding west toward the top of West Knoll. Twenty sampling stations with an area of 0.25 m^2 each were established.

Moths were first carefully picked from the snow surface. Next, the snow was excavated to a depth of 10 cm, and all moths were separated from the snow. Most moths were found near the surface. Next, we visually selected five areas on the snow where density of moths appeared to be especially high and sampled these areas using the same method. Random samples of moths were frozen for later chemical analysis.

Two solutions containing moths were prepared for chemical analysis at the University of Colorado Long-Term Ecological Research Water Quality Laboratory. Moths in each solution were ground into a fine paste using a mortar and pestle to break apart any visible pieces. A subsample of 11 moths (total weight of 0.173 g) was soaked in distilled, deionized water for 18 h. A second set of 10 moths (total weight of 0.1650 g) was soaked in distilled, deionized water for 2 h. Water was used to extract soluble nutrients. Two different time periods were used to estimate a minimum time necessary for soaking. Mean individual moth weight for 21 moths was 0.0161 g. Both solutions were stirred and filtered with a 0.45-μm membrane filter. For further analysis, the volume of filtrate was increased to 200 ml by adding deionized water. Cation analysis was performed with a Perkin-Elmer Model 2280 flame atomic absorption spectrophotometer. Anion analysis was performed by a Dionex 20101. Each solution was sampled and analyzed three times.

The following formula was used to calculate the amount of each compound input to a square meter of the alpine system: (ion in μg/g)(21 insects/m^2)(0.0161 g/insects) = X in μg/m^2 The letter X is the unknown compound being calculated.

RESULTS—Density of moths on the snow surface was 11.0/m^2 ($SD = 2.81$, $n = 20$); while those melted into the snow down to 10 cm below the surface had a density of 10.2/m^2 ($SD = 2.59$, $n = 20$). Total density was 21.2 moths/m^2 of surface area ($SD = 4.31$, $n = 20$) with the number ranging from 4 to 168 moths/m^2. Three areas selected for their especially high densities had 100, 132, and 168 moths/m^2. All values should be considered as minimums because some moths were removed by birds foraging on the snowfield, an effect we were not able to estimate.

Results of the anion and cation analysis are shown in Tables 1 and 2. For most ions, the solution made by the 2-h soaking period showed the highest concentrations. This was not true for Ca^{++}, K^+, and SO_4^{--}. The smaller concentrations in 18-h solution may represent adsorption to the glass wall of the beakers. For the remainder of the analysis, we used the highest concentration figure to determine if nutrient amounts might reach minimum levels to be of biological importance.

Our laboratory soaking crudely simulated leaching that occurs to insect bodies during decomposition in the field (note rain water is not deionized). It would not disassociate chitin since chitin is a very resistant substance, insoluble in water, alcohol, or dilute acid and only broken down only by *Bacterium chitinivorum* (Borror et al., 1981; Schelvis and van Geel, 1989). Moths,

TABLE 1—Results of anion and cation analyses. Solution 1 was soaked for 18 h, and solution 2 was soaked for 2 h. Each value is the mean of three tests run on a solution. Significant differences between solutions ($P < 0.05$) was found for each compound except F^-.

	Solution 1		Solution 2	
Compound	µg/g	±*SD*	µg/g	±*SD*
F^-	12.83	0.61	29.33	0.86
Cl^-	41.73	0.42	53.58	0.49
PO_4-P	818.57	7.46	846.39	3.25
SO_4^{--}	75.18	3.05	29.70	0.29
$(NO_2^- + NO_3^-)$	13.22	0.37	29.57	0.51
CA^{++}	54.55	1.21	46.06	0.97
Mg^{++}	59.52	0.81	65.05	0.44
Na^+	43.15	1.24	65.58	0.40
K^+	480.00	3.03	421.09	10.42

however, have a relatively small amount of chitin compared to other insects such as ants, beetles, and grasshoppers, so we do not believe eventual degradation of chitin, $C_{32}H_{54}N_4O_{21}$, will add significantly to nitrogen input. Bound nitrogen from chitin will eventually be added to the ecosystem, and amounts shown from the moth fallout should be considered as minimum estimates. Our laboratory process may imitate what actually occurs in nature, because most of the soluble chemical compounds would be released by initial leaching of soft parts of the body and exoskeleton.

DISCUSSION—The two soaking periods used for anion and cation analysis yielded different results perhaps because of adsorption to the glass wall of the beakers. For future tests, we recommend the use of teflon-coated beakers to prevent adsorption. Alternatively, the difference may represent real differences in the two samples, and it is regrettable that additional samples were not analyzed for each time interval when the event occurred.

Moth fallout was not uniform on the alpine tundra. Some high-density depositional areas that appeared to have resulted from flocking behavior of moths deposits were located on flat snow areas. Other dense concentrations of moths occurred because wind re-deposition and snowmelt runoff concentrated moth bodies in depressed areas. Localized areas with dense concentrations of moths had nutrient concentrations increased about eightfold, 168 moths/m² compared to the mean of 21.2 moths/m².

TABLE 2—Nutrient inputs from moth fallout. The largest value from the test solutions was used to calculate the nutrient inputs on an areal basis. Three solutions were analyzed for $(NO_2^- + NO_3^-)$ whereas two solutions were analyzed for the remaining compounds.

Compound	Test solution (µg/g)	Nutrient input (µg/m²)	mg/m²)
F^-	29.33	9.92	0.010
Cl^-	53.58	18.12	0.018
PO_4-P	843.39	285.15	0.285
SO_4^{--}	75.18	25.18	0.025
$(NO_2^- + NO_3^-)$	29.57	10.01	0.010
CA^{++}	54.58	18.44	0.018
Mg^{++}	65.05	21.99	0.022
Na^+	65.58	22.17	0.022
K^+	480.00	162.29	0.162

In addition to moths serving as a food source, external additions to alpine ecosystems of nitrogen and phosphorus compounds are important because of their potential limiting effect on primary and secondary production, However, nitrogen addition from the moth influx did not appear to be significant. Soluble nitrogen from moths (0.010 mg/m²) was 500-fold less than the mean annual amount of nitrogen fixed biologically on Niwot Ridge, 5 mg/m² (Wojciechowski and Heimbrook, 1984). Even on a community-by-community basis, soluble nitrogen from moths appears insignificant. The dry meadow community fixes the least nitrogen per year, but 66 times more (0.66 mg/m²) than moth input. Data are still needed on the cumulative effect of the continual influx of all windblown insects during a summer.

Estimates for phosphorus and potassium indicate potentially important additions to the tundra. Soluble phosphorus (PO_4-P = 0.285 mg/m²/event) from the moth infux was unexpectedly high (Irwin, 1982). Loading rates for bulk precipitation near our sample site averaged 5.5 mg/m²/year for soluble PO_4-P (Grant and Lewis, 1982). Phosphorus input from moths was 5% of the annual atmospheric input and represents an external, therefore possibly important addition to the alpine nutrient budget.

The PO_4-P carried by the moths may originate from fertilizers used on the Great Plains. In general, farmers in Colorado use nitrogen-based fertilizers. However, since alfalfa is a legume which can fix nitrogen, the main fertilizer used on alfalfa is Super Phosphate (F. Pierce, pers. comm.). Since fertilization in Colorado is <100 years old, we do not know if this new source of phosphorus has influenced primary production in the alpine.

We could not determine if phosphorus was on the insect or contained within its body. Winds, which blew the moths up to Niwot Ridge, may have deposited phosphorus-rich soil on moth bodies.

Soluble potassium, also detected at raised levels in our samples, is not a component of fertilizers. Larvae feeding on alfalfa grown on potassium-rich soils may have an increased potassium content when they molt to moths (F. Pierce, pers. comm.) or potassium soils may be deposited on their bodies.

Acid precipitation is a relatively new phenomenon in the Front Range which is poorly buffered against the effects of decreasing pH (Lewis and Grant, 1979, 1980; Kling and Grant, 1984). Litaor (1987) suggested that wind-borne calcium may serve to increase buffering capacity. Potassium from insects could have an additive effect on buffering capacity.

Episodic transport of insects to the alpine possibly creates important additions of PO_4-P and K^+. The phenomenon of PO_4-P enhancement may be relatively new to the alpine and may result from insects serving as vectors of agricultural practices on the Great Plains. Future episodic and continual influxes should be tested for soluble and insoluble nutrient inputs.

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LITERATURE CITED

ALEXANDER, G. 1950. The natural history of high altitudes. The Biologist, 33:91-97.

———. 1951. The occurrence of Orthoptera at high altitudes with special reference to Colorado Acaridae. Ecology, 32:104-112.

BORROR, D. J., D. M. DE LONG, AND C. A. TRIPLEHORN. 1981. An introduction to the study of insects. Saunders College Publishing, Philadelphia, Pennsylvania.

EDWARDS, J. S. 1972. Arthropod fallout on Alaskan snow. Arctic Alpine Res., 4:167-176.

———. 1987. Arthropods of alpine aeolian ecosystems. Ann. Rev. Entomol., 32:163-179.

EDWARDS, J. S., AND P. C. BANKO. 1976. Arthropod fallout and nutrient transport: a quantitative study of Alaskan snowpatches. Arctic Alpine Res., 8:237-245.

ELIAS, S. A. 1982. Paleoenvironmental interpretation of bark beetle fossils from two high altitude sites in the Colorado Rockies. Pp. 153-157, *in* Proceedings of the Third North American Paleontological Convention, I:153-157.

FAUST, R. A., AND T. J. NIMIOS. 1968. Soil microorganisms and soil nitrogen in the Montana alpine. Northwest Sci., 42:101-107.

FURNISS, M. M., AND R. L. FURNISS. 1972. Scolytids (Coleoptera) on snowfields above treeline in Oregon and Washington. Canadian Entomol., 104:1471-1478.

GRANT, M. C., AND W. M. LEWIS, JR. 1982. Chemical loading rates from precipitation in the Colorado Rockies. Tellus, 34:74-88.

GURNEY, A. B. 1953. Grasshopper Glacier of Montana. Annual Report Smithsonian Institute, 1952: 303-325.

HALFPENNY, J. C. (ED.) 1982. Ecological studies in the Colorado alpine: a Festschrift to John W. Marr. Univ. Colorado Inst. Arctic Alpine Res., Occas. Paper, 37:1-147.

IRWIN, R. L. 1982. The influence of soil nitrogen, phosphorus, and potassium on the germination and establishment of alpine plants. Unpubl. M.B.S. thesis, Univ. Colorado, Boulder, Colorado.

IVES, J. D. (ED.) 1980. Geoecology of the Colorado Front Range: a study of alpine and subalpine environments. Westview Press, Boulder, Colorado.

KLING, G. W., AND M. C. GRANT. 1984. Acid precipitation in the Colorado Front Range: an overview with time predictions for significant effects. Arctic Alpine Res., 16:321-329.

LEWIS, W. M., JR., AND M. C. GRANT. 1979. Relationships between stream discharge and yield of dissolved substances from a Colorado mountain watershed. Soil Sci., 128:353-363.

———. 1980. Acid precipitation in the western United States. Science, 207:176-177.

LITAOR, M. I. 1987. The influence of eolian dust on the genesis of alpine soils in the Front Range, Colorado. Soil Sci. Soc. Amer. J., 51:142-147.

MANI, M. S. 1968. Ecology and biogeography of high altitude insects. Ser. Entomol., W. Junk, The Hague, 4:1-527.

MAY, D. E. 1976. The response of alpine tundra vegetation in Colorado to environmental variation. Unpubl. Ph.D. dissert., Univ. Colorado, Boulder.

MAY, D. E., AND P. J. WEBBER. 1982. Spatial and temporal variation of the vegetation and its productivity on Niwot Ridge, Colorado. Pp. 35-62, *in* Ecological studies in the Colorado alpine: a Festschrift to John W. Marr (J. C. Halfpenny, ed.). Univ. Colorado Inst. Arctic Alpine Res., Occas. Paper, 37:1–147.

MAY, T. A. 1980. Animal ecology, overview. Pp. 430–436, *in* Geoecology of the Colorado Front Range: a study of alpine and subalpine environments (J. D. Ives, ed.). Westview Press, Boulder, Colorado.

SCHELVIS, J., AND B. VAN GEEL. 1989. A paleoecological study of mites (Acari) from a late glacial deposit at Usselo (The Netherlands). Boreas, 18: 237–243.

SHULLS, W. A., AND R. L. MANCINELLI. 1982. Comparative study of metabolic activities in three ecoregions of the Colorado Front Range, U.S.A. Arctic Alpine Res., 14:53–58.

SPAULDING, J. B. 1979. The aeolian ecology of White Mountain, California: windblown insect fauna. Arctic Alpine Res., 11:83–94.

SWAN, L. W. 1963. Aeolian zone. Science, 140:77–78.

———. 1967. Alpine and aeolian regions of the world. Pp. 29–54, *in* Arctic and alpine environments (H. E. Wright and W. H. Osburn, eds.). Indiana Univ. Press, Bloomington, Indiana.

WELLINGTON, W. G. 1945. Distribution of insects in the atmosphere. Canadian Entomol., 77:7–15, 21–28, 44–49, 69–74.

WOJCIECHOWSKI, M. F., AND M. E. HEIMBROOK. 1984. Dinitrogen fixation in alpine tundra, Niwot Ridge, Front Range, Colorado, USA. Arctic Alpine Res., 16:1–10.