INTRODUCTION

During the past two hundred years pollination ecology has been the subject of considerable investigation. However, the energetic aspects of the plant-pollinator interaction have been largely overlooked (Heinrich and Raven 1972). Most of the reported work has been descriptive (Knuth 1906, 1908; Muller 1883). This work has resulted in the description of "pollination syndromes" whereby plants are classified on the basis of appearance (morphology, color, scent, and time of day at which they are open) as to the probable class of pollinator they attract (Proctor and Yeo 1972, Faegri and van der Pijl 1966, Baker 1961).

Only recently has the focus of pollination ecology shifted to the quantitative aspects of the interaction (Heinrich 1972a, 1972b). Energy, in the form of nectar sugars, is the ultimate attractant eliciting visitation of the flower by the majority of pollinators. In fact, nectar is the principle source of energy for pollinating organisms, without which, they would be unable to function. It would seem likely, therefore, that a plant's energetic output and its pollinator's energetic requirement have evolved to become similar to as high a degree as floral and pollinator morphology (Hickman 1974).

This energetic coevolution can be achieved in a manner similar to morphological coevolution. A reduction in the supply of nectar will restrict a flower's visitors to only those animals able to make an energetic profit.

Researchers investigating pollination energetics have concentrated their efforts on the pollinator's foraging strategy. They have analyzed the consumption of energy by the forager with regard to changing environmental conditions and changing and static nectar availability (Heinrich 1970, 1972a,b,c, 1975a, 1976; Hainsworth and Wolf 1972; Watt et al. 1974; Oster and Heinrich 1976; Oster 1976). However, little is known about the evolutionary factors that influence the pattern of nectar secretion in a plant species.

Selection should favor plants maximizing the transfer of pollen to conspecific stigmas. This is accomplished if the plant is visited by the largest numbers of host specific pollinators available. Energetic or morphological restriction of the number of pollinator species able to utilize a plant species' energy (nectar reward) reduces the interspecific competitive interactions of those pollinators.

Such reduction in competition among pollinators can increase the average reward a forager can expect. This should lead to an increase in host specificity since the forager can expect a greater energy reward relative to energy expended (Emlen 1966, Schoener 1974). If a plant is unable to replenish nectar rapidly, it must limit access of nectar to those organisms which are effective pollinators. Thus, increased energy offerings are often accompanied by morphological restriction which excludes ineffective pollinators (Heinrich 1975b, Mosquin 1971). Similar restriction could be achieved by reduction in the amount of energy produced. This may serve a triple function:

1) it will reduce the number of species able to make an energetic profit, thus acting in a manner similar to morphological restriction (Hickman 1974).

2) it will increase the number of visits necessary to satiate a forager, thus increasing the outcrosses a pollinator can accomplish (McGregor et al. 1959, Hawkins 1961).

3) it will reduce the energy expended by the plant (the extent to which this is important is doubtful) (Shuel 1955, Street and Opik 1970).

The greatest amount of pollen is transferred (and seed set) if pollinators must visit many plants in order to obtain a certain amount of nectar energy (Hawkins 1961, Pedersen 1954, Heinrich and Raven 1972). Thus, selection should favor the reduction of nectar energy in flowers to the minimum necessary to attract pollinators.

Heinrich and Raven (1972) posed several questions about how a plant species' nectar secretion might be expected to change in relation to various biotic and physical factors. The influence of competition for pollinators (Mosquin 1971, Heinrich 1975b, Hocking 1968), pollinator energetics (Hickman 1974), and flower density (Heinrich and Raven 1972) on nectar secretion have been investigated; however, the influence of increased energetic requirements by pollinators at low temperatures and its ecological significance on plants has not been examined.

The quantity of nectar sugar produced by plants can range from that which is barely detectable by human taste, to an amount so large that it has been used as a source of sugar for humans (Shuel 1955a). Many of the dissimilarities in nectar secretion can be explained in terms of the differences between plant species. Species subjected to different sets of selective forces adjust their physiological responses to maximize reproductive success. In addition, local environmental conditions can favor different patterns of nectar secretion in different populations of a plant species (Clausen et al. 1948). Do plants regulate their nectar secretion according to daily meteorological fluctuations? Is there a metabolic system in the plant which responds to daily changes in weather and which influences nectar secretion so as to increase reproductive success?

Additionally, are all the individuals of a population influenced similarly by environmental conditions?

If not, is individual variation due to adaptive genetic variation (Schoener 1967)? Do different individuals within a population achieve optimal fitness (measured as reproductive success) under different meteorological conditions?

Considerable effort has been expended to determine the role of physical factors in influencing nectar secretion.

Temperature has been extensively investigated (Percival 1946, Weast 1973, Walker 1974, Bailey and Fieger 1954, Demuth 1923, Vansell 1939). The effect of temperature does not seem to be consistent either within or between species.

It is believed that there is no effect of relative humidity on nectar secretion; but that once secreted, nectar volume and concentration are strongly influenced by the amount of moisture in the air (Scullen 1940, 1942; Oertel 1946, Park 1920, Vansell 1940).

The addition of potassium to soil results in an increase in nectar sugar production. However, excessive fertilization with phosphorous or nitrogen results in reduced sugar produced (Shuel 1967). Slightly greater than average rainfall has been positively correlated with increased nectar secretion (Shuel 1967).

Shuel (1955a) reports that the amount of solar radiation to which plants are exposed is also very important.

Heinrich (1970, 1972a,b) has shown that bumblebees and hawkmoths regulate their thoracic temperature to a level higher than ambient. This heat is in excess of that produced solely by flight. Plants pollinated by such "homeothermic" visitors must supply the insect with more energy at low ambient temperatures or the insect will not be able to make an energetic profit and may forego visitation (Heinrich 1972b).

Therefore, many factors may influence nectar secretion. However, to the extent that the effect of ambient temperature differences on pollinators has exerted a significant effect on nectar secretion in plants, three possible situations may exist:

1) a constant high rate of nectar production (this will reduce the number of plants visited by a pollinator and can be wasteful of energy).

2) a constant low rate of nectar production (pollinators may not visit the plant at low temperatures).

3) a variable rate of nectar production inversely correlated with temperature.

Thus, plants visited by "homeotherms" such as bumblebees and hawkmoths might be expected to increase their nectar energy output at low temperatures.

The purpose of this study is to test this hypothesis.