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False Satiation: The Probable Antiherbivory Strategy of *Hoodia gordonii*

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ABSTRACT

The succulent, thorny, South African desert plant *Hoodia gordonii* and several other species of the genus, as well as *Pectinaria maughamii* were found to be appetite suppressants and thirst quenchers. The appetite-suppressant drug from *Hoodia* species increases the content of ATP by 50-150% in hypothalamic neurons, thus activating an anorectic mechanism. We propose that these plants have evolved such compounds as a defense against herbivory, causing false satiation. We hypothesize that the same principle operates in other plants, such as *Thaumatococcus daniellii* that produces nature's sweetest known molecule (the protein thaumatin). *Hoodia* and similar plants thus express a previously unknown mechanism of anti-herbivore defense – false satiation.

Keywords: defense, herbivory, *Hoodia*, satiation

Because plants are sessile and they are the main producers of terrestrial biomass, they suffer from the constant pressure of various types of herbivory by animals. In response, plants have evolved a rich arsenal of anti-herbivore defense mechanisms, e.g., chemicals (Biere *et al*. 2004), spines (Grubb 1992), aposematism and defensive coloration (Lev-Yadun 2001; Lev-Yadun *et al*. 2004; Lev-Yadun 2006), mutualism with ants (Huxley and Cutler 1991) and attracting predators of herbivorous insects (Kessler and Baldwin 2001).

A succulent, thorny, cactus-like plant from the arid parts of South Africa, *Hoodia gordonii*, a member of the Asclepiadaceae, and several other species of the genus, as well as *Pectinaria maughamii* (Archer and Victor 2003), were found to be appetite suppressants and thirst quenchers. These plants have been used by the indigenous San people during their field trips for generations to overcome hunger and thirst. The Council for Scientific and Industrial Research in South Africa patented the appetite-suppressant drug P57 from *Hoodia* species, and *Hoodia* extracts are orally prescribed to treat human obesity. The putative active component is a trirhabinoside, 14-OH, 12-tigloyl pregnane steroidal glycoside (M_w = 1008). The compound increases the content of ATP by 50-150% in hypothalamic neurons, thus activating an anorectic mechanism (MacLean and Luo 2004). Feeding lean and obese rats with the *Hoodia* extracts resulted in weight loss in both groups (Tulp *et al*. 2001, 2002).

The broad public interest in these plants due to their commercial potential in the diet industry is obvious, but there seems to be a special scientific issue involved, i.e., the reason for the evolution of this trait. We propose that these plants have evolved such compounds as a defense against herbivory. Several types of plant chemical defense are already known: Poisoning of herbivores by toxins is a very common defense (Janzen 1971; Bryant *et al*. 1991; Kursar and Coley 2003), inhibition of digestion by various molecules such as tannins (Green and Ryan 1972; Bryant *et al*. 1991), olfactory aposematism (Eisner and Grant 1981) and attracting predators and parasitoids of herbivores by various volatiles (Kessler and Baldwin 2001). Real herbivore satiation by production of exceptionally large numbers of seeds in certain mast years is a well-known plant defense from seed predation (Janzen 1976; Kelly and Sork 2002). Satiation may influence the diet of animals considerably (Pyke 1984). Causing false satiation, as happens with *Hoodia* and certain other plants, might be no less rewarding than other types of defense. The benefits for the plant are clear: in the short run, an herbivore that grazes on the plant will eat less and will damage the plant less. Herbivores that graze such plants may become weaker in time because they will repeatedly eat less and thus likely be prone to disease and predation or suffer from lower reproduction. We hypothesize that the same principle operates in other plants, such as *Thaumatococcus daniellii* that produces nature's sweetest known molecule (the protein thaumatin) (Cagan 1973; Waliszewski *et al*. 2005), and probably via other molecules in other plants that are frequently identified as producing intensive sweeteners (Bassoli 2004). Although plants regenerate better than animals after being partly eaten (Ohgushi 2005) and may benefit more at the individual level from such a trait, theoretically, animals (especially clonal or social) might also employ the same principle of inducing false satiation in their predators to reduce predation. We thus propose that *Hoodia* and similar plants express a previously unknown mechanism of anti-herbivore defense – false satiation.

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