The Cost of Being Dormant in the Tropics

Daniel H. Janzen, Don E. Wilson

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Daniel H. Janzen

Department of Zoology, University of Michigan, Ann Arbor, Michigan 48104 U.S.A.

and

Don E. Wilson

National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. 20560 U.S.A.

ABSTRACT

The roots, stems, and twigs of *Jacquinia pungens* were found to lose as much as one-half of their stored carbohydrate reserves when leafless during the rainy season. This finding implies that dormancy can be an expensive way to avoid an inimical environment.

Jacquinia pungens A. Gray (Theophrastaceae) is an understory shrubby tree in Central American deciduous forests. In Costa Rica, it produces leaves at the beginning of the dry season (December) and drops them about six months later at the beginning of the rainy season (May-June) (Janzen 1970). In this paper we examine the hypothesis that the rainy (dormant) season is a period of substantial stress to the plant, as measured by metabolic expenditures at this time. The cost to *J. pungens* of rainy season dormancy is a special case of the general problem of understanding the cost of being dormant at high tropical temperatures. This dormancy contrasts strikingly with the apparent low metabolic cost of dormancy for a poikilothermic tree during the cold season in temperate zones. We chose *J. pungens* for this study because of its abundance, small size at reproductive maturity, conspicuous starch storage, lack of sexual activity while leafless, and potential for suggesting minimal maintenance costs for a woody plant during the rainy (coolest) time of year in the lowland tropics.

METHODS AND STUDY AREA

Twig, main stem, and root segments were collected from each of five 1.5-2.0 m tall *J. pungens* shrubs on seven dates (table 1). Twig segments were from the previous year's growth; main stem segments were 2-4 cm diameter and from about 30 to 80 cm up the trunk; and the root segments were from the tap root at a point 10-20 cm below the ground and the same diameter as the main stem segments. *J. pungens* is exceptional among tropical deciduous forest understory shrubs in that it has a very deep and large tap root (Janzen 1970). The shrubs were sacrificed when sampled.

The woody segments (including the thin bark) were diced and placed in a drying or kitchen oven within 24 hours. After drying to approximately constant weight at 80-100° C (2-10 days), they were sealed in plastic bags. The samples were later analyzed for total available carbohydrate (TAC) by J. Menke and M. J. Trlica (Range Science Department, Colorado State University, Fort Collins, Colorado 80521); see Trlica and Cook (1971) and included references for methods. The TAC for the entire plant (table 1) was calculated by using an estimated ratio of 5:10:1 for the dry weight of root:main stem:twigs in a *J. pungens* about 3 m tall. It should be remembered that *J. pungens* has a very peculiar root system in that there are no lateral roots near the surface (Janzen 1970).

Shrubs were chosen that appeared representative

TABLE 1. *Total available carbohydrate* (TAC) *in mg per g of* Jacquinia pungens *twig, stem and root segments. Each value is the average of five samples and the same five shrubs were used for twig, stem and root segments on a given date. See text for calculation of* TAC *for entire shrub.*

	22-I-'71	17-III-'71	20-V-'71	24-VII-'71	4-X-'70	12-XI-'70	12-XII-'70
Twig values	*16.0*[a]	*41.1*[a]	*30.5*[a]	30.1	25.1	18.4	*16.0*[a]
Main stem values	*39.6*[a]	*53.6*[a]	*68.1*[a]	60.1	53.5	30.9	*23.2*[a]
Root values	*85.9*[a]	*103.9*[a]	*113.4*[a]	114.4	107.0	69.1	*43.7*[a]
Total value calculated for a 10 kg shrub (g)	*530.0*[a]	*689.5*[a]	*803.4*[a]	756.8	689.2	423.7	*293.3*[a]

[a] The shrubs had leaves at the time of sampling.

of the general population with respect to health and state of leaf drop, flowering, fruiting, etc. Flowers or fruits were present on the plants sampled only during the months of December to May. Most of the *J. pungens* had a nearly full leaf crop by the end of December and all did by January (fig. 1 E). All were growing in the understory of a 50-year or older deciduous 30-hectare forest on a low knoll approxi-

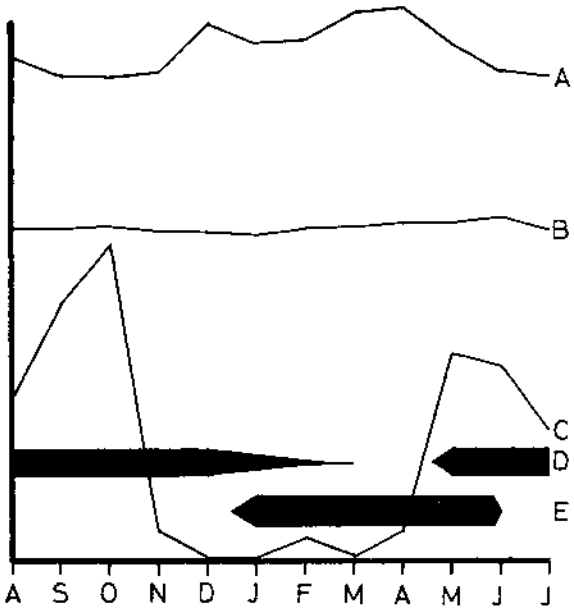

FIGURE 1. A. Mean monthly maximum temperature in C° for Cañas, highest value about 33 C°. B. Mean monthly minimum temperature in C° for Cañas, lowest value about 21 C°. C. Distribution of mean monthly rainfall at Cañas (average for 1951-1960), wettest month is about 425 mm. D. Extent of foliation of hillside forest canopy. E. Extent of foliation of *Jacquinia pungens*.

mately in the center of Finca La Pacifica, north of Cañas, Guanacaste Province, Costa Rica. This forest is within a few hundred meters of Janzen's (1970) study area. The annual rainfall at Finca La Pacifica is about 1900 mm per year, and almost all of it falls between the last week of April and the middle of December (fig. 1 C). The deciduous forest is in full leaf within a week or two after the first heavy rains. The leafy canopy casts heavy shade until December (fig. 1 D). Leaf drop is gradual after this date. The maximum light intensity at ground level in the forest (5000-6000 foot-candles at mid-day, Janzen 1970) is not attained until about the middle of March, but there is a conspicuous increase in the amount of light at ground level by mid-January. Monthly maximum and minimum air temperatures for Cañas were reported earlier (Janzen 1967) but are illustrated in figure 1 A and B.

RESULTS

The TAC in the shrub as a whole declines from about the time the leaves start to drop until the next set of leaves is produced. The steady decline from 20 May to 12 November may be attributed to respiration losses (dormancy maintenance metabolism) while that between 12 November and 17 December may be due to the cost of making a new set of leaves and twigs as well. While it is possible that some respiratory costs from May to November were due to leaf bud growth, this seems unlikely as the buds are already formed in May yet remain extremely small during the rainy season. Some of the rainy season respiratory losses may also be associated with mineral uptake deep in the soil. However, whatever their use, the shrub's carbohydrate reserves by December (shortly after leaf production) are reduced to about one-third their level at the end of the photosynthetic season in May.

The twigs, main stem, and roots show a pattern similar to that of the shrub as a whole. However, it appears that the main stem and root tissue TAC reserves are replenished by the plant before those of the twigs. Several other more subtle trends are suggested by the data but will not be pursued because a sample size of only five plants per sample does not seem large enough to override intraspecific variation except in the overall trend.

DISCUSSION

These results generally support the hypothesis that even poikilothermic organisms cannot readily avoid respiratory energy loss when dormant during warm weather (cf. Janzen 1973 with respect to tropical insects). While a *J. pungens* shrub could conceivably turn itself off as thoroughly as can a dormant seed, it would probably have to encase itself in a "seed coat" to do so, if it were to avoid death by desiccation. Such a seed coat (e.g., very corky bark and lignified root epidermis) might well cost more than the carbohydrate burned during the rainy season and be incompatible with desired physiological processes during the dry season. In an earlier discussion of *J. pungens*, it was pointed out that the upper twigs of the shrub die during the rainy season if the surrounding forest has been cut down, with the consequence that the leafless twigs are exposed to direct insolation (Janzen 1970). In view of the severe reduction in TAC during the dormant period

even in shaded twigs, it seems likely that these heated (insolated) twigs are literally starving to death.

These results bring to mind the possibility of an overlooked advantage of the evergreen behavior displayed by certain species of deciduous forest trees (e.g., *Hymenaea courbaril* L., *Manilkara achras* L., *Licania arborea* Seem., *Brosimum alicastrum* Swartz, *Ardisia revoluta* HBK, *Byrsonima crassifolia* (L.) HBK, *Ficus* spp., *Andira inermis* (Wright) Urban). The shade from their own leaves cast on twigs and branches may substantially lower respiratory costs.

In conclusion, we should emphasize that dormancy by a poikilotherm during a tropical inimical season may be far more costly than during a temperate-zone winter. Not only does the warm air have increased drying power, but it also causes the organism to expend substantial amounts of energy even when appearing to be doing nothing.

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