Original papers

Fire adaptation in *Neblinaria celiae* (Theaceae), a high-elevation rosette shrub endemic to a wet equatorial tepui

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Summary. *Neblinaria celiae* (Theaceae), a rosette shrub endemic to the exceedingly rainy summit of remote Cerro de la Neblina in southern Venezuela, has a previously undescribed set of adaptations to fire. Its growth form entails sparse branching, massive terminal leaf rosettes, and thick bark. It is highly fire-tolerant, with a survival rate of 93% in a stand recently ignited by lightning, vs. 0% in seven co-occurring woody species. Survival increases sharply with rosette height, favoring a sparsely branched habit that would maximize the rate of upward growth through the sparse fuel layer supported by a sterile substrate. Thick bark and massive rosettes help protect cambial and foliar meristems from brief exposure to high temperatures. Rosettes on shorter plants are exposed to greater damage from fire near the ground and, as expected, are bigger and impound more rainwater; the greater number of leaves nearly balances the greater leaf mortality caused by fire. We relate *Neblinaria's* growth form to its dominance atop Neblina, to a general model for the evolution of sparse branching, and to the evolution of growth form in other tepui plants.

Key words: Fire – Rosette shrubs – Tropical-alpine vegetation – Neblinaria – Guayana Highlands

The Guayana Highlands of northern South America are of considerable evolutionary interest. The isolated, cliff-lined summits of the tepuis, or sandstone table mountains, of this region support floras with a high incidence of local endemism and unusual growth forms (Gleason 1931; Steyermark 1966, 1967; Steyermark and Maguire 1967, 1972; Maguire 1970). One of the most bizarre growth forms found on these extremely humid and infertile summits is that of *Neblinaria celiae* Maguire (= *Bonnetia maguireorum* Steyermark) (Theaceae:Bonnetioideae), known only from plateaus at 1,700–2,200 m elevation on Cerro de la Neblina (0°50′N, 66°0′W) in southernmost Venezuela (Maguire 1955; Maguire et al. 1972; Cronquist 1980; Steyermark 1984). *Neblinaria* is monotypic, with closest relatives in the large genus *Bonnetia* and related segregates *Neogleasonia* and *Neotatea* (Maguire 1955, 1970; Steyermark and Maguire 1967, 1972; Maguire et al. 1972; Steyermark 1984).

Neblinaria is an unbranched to sparsely branched, can-

delabra-like woody plant, 1–3 m in height, with massive, artichoke-life leaf rosettes surmounting each ascending branch (Fig. 1a, b). Its bark is extremely thick (ca. 1 to 4 cm), spongy, and deeply fissured (Fig. 1c). *Neblinaria* often is quite common, forming nearly monospecific stands over leached sandstone on the mist-drenched plateaus of Neblina (Fig. 1d). We thus became interested in determining what ecological factors may have favored the evolution of its unusual growth form and its current dominance.

Theory

Two sets of factors might favor an unbranched or sparsely branched habit. First, such a growth form could be favored by any factor that places a strong selective premium on height growth, because branching diverts energy from a plant's leader and tends to decrease height growth, at least in the short term (Givnish 1978, 1984). Specific factors that might favor rapid height growth include herbivores or other agents (e.g., floods, fires, ground frosts, smothering bryophyte growth) that prey preferentially on short plants, as well as canopy gaps that close quickly and favor rapidly growing individuals in shade-intolerant species. Second, a sparsely branched habit might be favored if the protection afforded a bud or shoot axis increases sharply with the number of leaves packed closely around it. This latter hypothesis has been advanced to account for the evolution of monocauly in *Espeletia, Dendrosenecio*, and other tropical alpine shrubs exposed to brief nightly frosts, in which living leaves curl about the terminal bud at night and insulate it from thermal extremes, and dead leaves remain attached to the shoot axis and prevent the xylem and pith from freezing (Hedberg 1964; Smith 1974, 1979, 1981; Beck et al. 1982, 1984; Goldstein and Meinzer 1983; Goldstein et al. 1984; Meinzer and Goldstein 1986). However, this hypothesis could have more general applicability. Frost appears not to occur on Cerro de la Neblina at the elevations inhabited by *Neblinaria*, based on Maguire's (1955) meteorological observations. Maguire (1955) reports night-time thermal minima of roughly 5° C in his summit camp near stands of *Neblinaria* at 1,800 m elevation. Furthermore, based on a wet adiabatic lapse rate of 0.6° C/100 m elevation, and an estimated night-time minimum of 17° C at lowland (ca. 200 m) sites not immediately around the base of the mountain, the estimated night-time minimum tem-

Table 1. Density, height distribution, and survival of *Neblinaria* and co-occurring woody species after fire, as judged by numbers of live and dead stems (rosettes in the case of *Neblinaria*) in burnt stand. Average number of live stems or rosettes per 25 m²-quadrat indicated in bold-face; number of dead stems/rosettes indicated in roman-face

	Height class (m)					Survival rate
	0.0–0.1	0.1–0.5	0.5–1.0	1.0–1.5	>1.5	
Bonnetia neblinae	0.5	2.5	3.7	2.1	0.6	0.0
Everardia montana	10.7	35.0	0.8	0.0	0.0	0.0
Glossarion rhodanthum	0.0	0.1	0.1	0.1	0.0	0.0
Macairea neblinae	0.0	0.3	0.4	0.0	0.0	0.0
Myriocladus neblinaensis	0.0	0.1	1.1	0.1	0.1	0.0
Neblinaria celiae (live)	**2.2**	**33.6**	**67.2**	**10.7**	**0.0**	93.1
Neblinaria celiae (dead)	1.9	3.7	2.5	0.3	0.0	
Pagamiopsis maguirei	0.1	3.9	2.5	1.4	0.2	0.0
Rutaneblina pusilla	0.2	3.9	0.6	0.5	0.0	0.0

perature should be 8.0° C near *Neblinaria's* lower elevational limit of 1,700 m, and 5.0° C near its upper limit at 2,200 m. Climatic records for southern Amazonas territory (Huber 1982; Huber et al. 1984) indicate a mean annual rainfall of roughly 3,000 mm at about 200 m elevation, distributed rather evenly through the year; adiabatic cooling leads to greater humidity, cloudiness, and rainfall atop the tepuis (Brewer Carias 1976).

Neblinaria's thick bark suggested that adaptation to fire – however unlikely in view of the high humidity and rainfall atop Neblina – might be related to the evolution of its unusual growth form. During helicopter reconnaissance of the remote Neblina massif in January 1985, an opportunity arose to test this idea. Two plateaus roughly 2 km² in area (0°54'40"N, 66°2'30"W; 1,750 m elevation), covered by a mixture of *Neblinaria* and several other woody species, were discovered that had been burnt the past two months, as indicated by previous reconnaissance by C. Brewer Carias (personal communication). The fires appear likely to have been ignited by lightning, because (i) no humans are resident atop or within ten km of Neblina, (ii) the mountain top is isolated from the surrounding lowlands by cliffs and extremely steep slopes, and (iii) we observed frequent lightning strikes in the area. Studies were initiated in and adjacent to these burned areas to determine whether *Neblinaria* could survive fire, and to evaluate the adaptive value of its branching pattern, leaf rosette form, and thick bark.

Methods

Vegetation was sampled in ten randomly chosen, 5 × 5 m plots in burnt and unburnt stands near the edge of one burnt area. All woody individuals, living and recognizable dead, were tallied by species and height class. Height classes were 0.0–0.1 m, 0.1–0.5 m, 0.5–1.0 m, 1.0–1.5 m, 1.5–2.0 m, and 2.0–2.5 m. Few woody plants (*e.g., Bonnetia neblinae*) exceeded 1.5 m height in the study plots.

For *Neblinaria*, the number of rosettes per individual, their height, and live/dead status were also noted. The number of live expanded leaves in each rosette was tallied as a function of rosette height in thirty *Neblinaria* in burnt and unburnt stands. In addition, in unburnt stands, rosette diameter and the volume of rainwater impounded by each rosette was tallied as a function of rosette height. In burnt stands, bark thickness was measured at various points be-

tween the rosette and ground in ten living and ten dead *Neblinaria*.

Results

Fire tolerance. *Neblinaria* rosettes showed 93.1% survival after fire, vs. 0.0% aboveground survival and very little resprouting in all other woody species (Table 1; $\chi^2 = 1,613.3$, $P < 0.001$ for 7 d.f.). Survival after fire was assessed by computing the proportion of live individuals in populations of each woody species in the burnt stand. This method is accurate if the fire that struck that stand was not so severe as to burn completely the stems of some dead individuals, and if few individuals were dead preceding the fire. These assumptions appear valid based on a comparison of the composition and structure of the burnt and unburnt stands, because (1) the species present in each are almost identical; (2) stems were charred only superficially, so that even fine stems were recognizable and countable after fire (excepting, in some cases, *Rutaneblina*); and (3) few dead individuals of any species occur in the unburnt stand.

These data demonstrate *Neblinaria's* ability to survive fire, as well as the competitive advantage it has in the presence of fire. The woody species found with *Neblinaria* would be expected to suffer greater damage from fire, because they have much thinner trunks, branches, and bark, more slender leaf rosettes, and (except *Bonnetia neblinae*) are generally shorter in stature. A few herbaceous plants - notably species of *Brocchinia* (Bromeliaceae), *Heliamphora* (Sarraceniaceae), and *Stegolepis* (Rapateaceae) – resprout vigorously after fire from leaf rosettes or underground rhizomes invested by sclerotized leaf tips, water-storing pitchers, or mucilage-filled sheathing leaf bases, respectively (Fig. 1e).

Fire adaptation. The probability of a leaf rosette surviving a fire increases sharply with rosette height (Table 2). Rosettes within 10 cm of the ground showed 46.3% mortality, whereas those at least 50 cm above the ground suffered only 3.5% mortality ($\chi^2 = 137.0$, $P < 0.001$ for 1 d.f.). Presumably, this results because the extremely infertile sandstone substrate, leached by heavy rainfall under humid conditions, can support only a sparse fuel layer of short shrubs and herbs. If a plant can elevate its delicate meristems above this layer, they are likely to avoid the greatest heat and
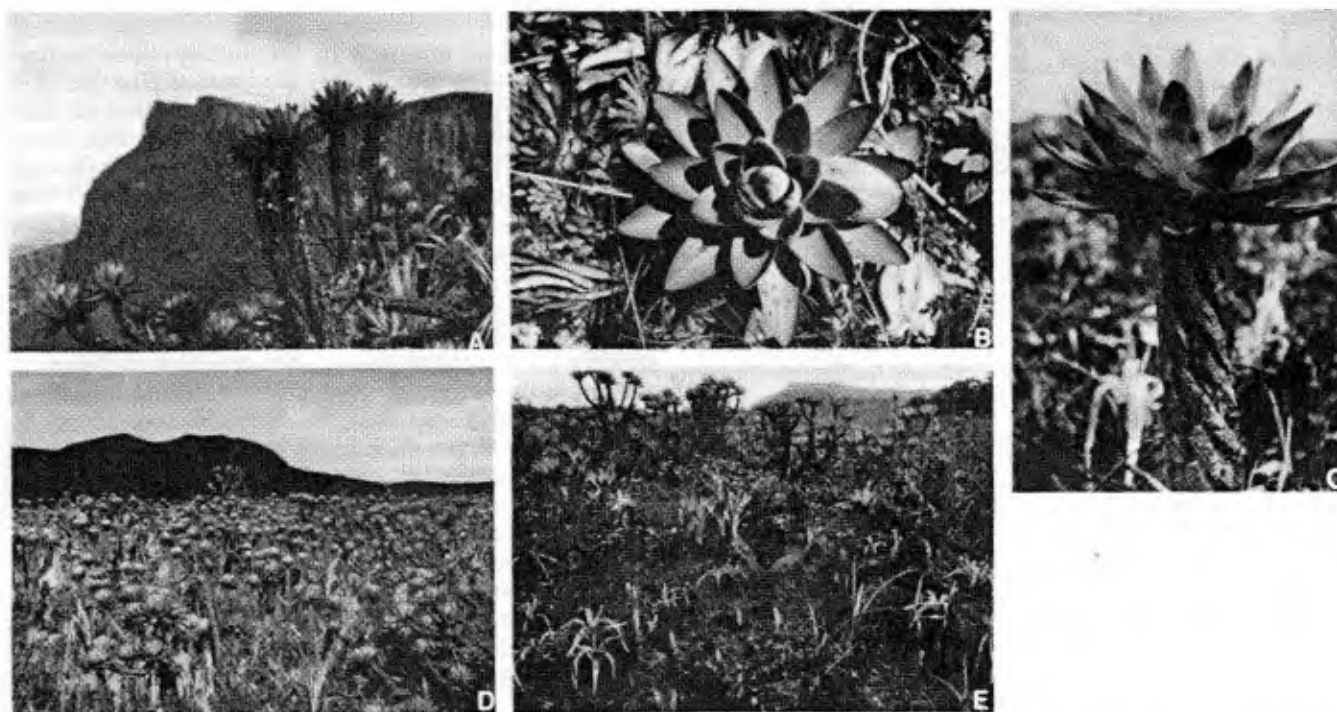
Fig. 1. A Growth habit of *Neblinaria celiae*, with northern scarp of Cerro de la Neblina in background; **B** close-up of young leaf rosette; **C** rosette and bark surface on upper stem from individual in burnt stand (note scorched leaf tips) **D** plateau dominated by stand of *Neblinaria*, 1,800 m elevation **E** view from boggy swale into recently burnt *Neblinaria* stand, with resprouting herbs *Brocchinia*, *Heliamphora*, and *Stegolepis* in foreground

Table 2. *Neblinaria* rosette mortality in burnt stand as a function of rosette height

Rosette height (m)	Number of *Neblinaria*:		Percent mortality*
	Alive	Dead	
0.0–0.1	22	19	46.3ᵃ
0.1–0.5	336	37	9.9ᵇ
0.5–1.0	672	22	3.2ᶜ
1.0–1.5	107	3	2.7ᶜ

* Different letters indicate mortality rates are significantly different at the 95% confidence level

Table 3. Rosette survival in branched and unbranched plants of different heights*

Rosette height (m)	Number of *Neblinaria*:		Number of branches
	Alive	Dead	
0.0–0.1	20	17	1
	2	2	>1
0.1–0.5	154	15	1
	182	22	>1
0.5–1.0	92	3	1
	580	22	>1
1.0–1.5	9	0	1
	98	3	>1

* No differences in mortality between branched and unbranched shoots within a given height class are significant at the $P < 0.05$ level, as judged by χ^2 or Fisher exact tests

potential damage from the brief fires sweeping through the habitat. The sharp increase in rosette survival with height puts a selective premium on height growth, and would appear to be an important factor promoting sparse branching. Note, however, that branched and unbranched *Neblinaria* with rosettes at a given height face indistinguishable chances of survival (Table 3). Branching *per se* does not decrease survival, but should decrease the rate of height increase, and thus prolong a plant's exposure to greater fire intensity and mortality near the ground.

Neblinaria bark is quite thick, averaging a maximum of 2.2 ± 0.2 cm on woody stems with a maximum diameter of 8.5 ± 1.6 cm in stands not recently burnt. Bark thus comprises roughly three-quarters of a stem's cross-sectional area. It also has numerous air cavities that increase its insulating capacity; charring is limited mainly to superficial layers under the fire conditions observed. Among *Neblinaria* in the burnt stand, the bark is thicker at the base of surviving plants than dead plants, and the diameter of the woody cylinder is thicker at the base of surviving rosettes. Bark thickness averages 20.4 ± 8.6 mm at the base of live, burned *Neblinaria* stems, and 9.3 ± 3.8 mm at the base of dead, burned stems ($P < 0.01$, 2-tailed t-test, 18 d.f.). Thickness of the woody cylinder (excluding bark) immediately below the leaf rosette averaged 35.5 ± 4.7 mm in living stems and 17.2 ± 3.7 mm in dead stems ($P < 0.001$, 2-tailed t-test, 18 d.f.). These data appear to confirm the expected importance of thick bark and a large stem diameter in preventing combustion and insulating a plant from the brief exposure to high temperatures expected during tepui fires.

The massive leaf rosette of *Neblinaria* also appears, based on qualitative and quantitative observations, to be of adaptive value in resisting fire damage. Observations
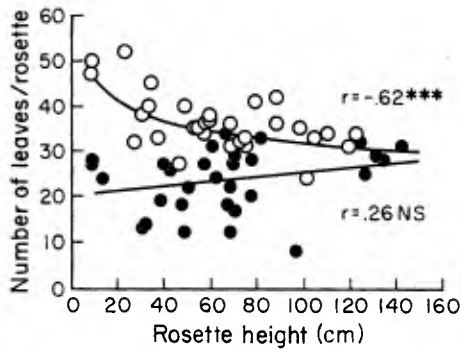
Fig. 2. Number of leaves per rosette as a function of rosette height in burnt (o) and unburnt (o) stands of *Neblinaria celiae*
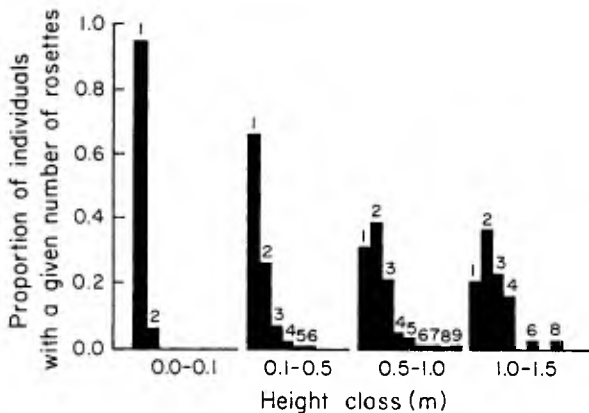

Fig. 3. Proportion of *Neblinaria* individuals in each height class with different numbers of rosettes. Numerals above each bar indicate plants with the corresponding number of rosettes

in burnt stands indicated that many outer leaves of a rosette could burn and the rosette still survive, with its terminal bud insulated by the numerous inner layers of expanded and unexpanded leaves. Copious amounts of rainwater impounded by the outer leaves (mean $= 107 \pm 67$ ml) should also slow their combustion and the spread of heat into the rosette core.

A corollary of this hypothesis is that shorter plants, exposed to greater thermal extremes during fire, should have larger rosettes. Indeed, among plants not exposed to fire recently, rosettes increase in diameter, leaf number, and volume of impounded rainwater with increasing proximity to the ground (Fig. 2). Data were fit to linear and log-log principal axis regressions, and the better fit chosen for each pair of parameters, with 28 d.f. in each case. For *Neblinaria* in unburnt stands, ln (no. of leaves/rosette) $= -0.160*$ln (height) $+ 4.216$ ($r = -0.618$, $P < 0.001$); rosette diameter $= -0.159*$height $+ 32.01$ ($r = -0.470$, $P < 0.01$); and impounded volume of rainwater $= -4.341*$height $+ 380.1$ ($r = -0.406$, $P < 0.05$). For recently burnt stands, no. of leaves/ rosette $= -0.53*$height $+ 19.99$ ($r = 0.264$, $P > 0.05$).

Furthermore, there is no significant tendency for the number of leaves per rosette to vary with rosette height in *Neblinaria* recently exposed to fire (Fig. 2). The difference between the regressions of leaf number/rosette on rosette height for burnt and unburnt stands yields the expected number of leaves destroyed by fire as a function of rosette

height. This analysis confirms that the potential damage caused by fire, as measured by the number of leaves destroyed, accelerates greatly near the ground (Fig. 2). This trend parallels that indicated by the mortality data. The greater leaf number found, before fire, in shorter plants appears to almost to balance the increase leaf loss they face (lower curve in Fig. 2). If the number of leaves borne by *Neblinaria* did not vary with stem height, so that plants shorter than, say, 10 cm tall had only the observed pre-fire mean across all plants of 36.4 leaves/rosette – rather than the observed 48.5 leaves per rosette – they would retain very few (mean $= 8.0 \pm 6.2$) fully expanded leaves and presumably be exposed to heavy mortality. Although factors other than fire (e.g., more favorable evaporative regime or nutrient status) may also favor increased rosette size in short individuals, our data clearly suggest that such behavior would, in addition, confer an adaptive advantage in surviving fire.

Both sets of factors that favor the evolution of unbranched or sparsely branched stems thus appear to be operating in *Neblinaria*. Heavy fire-induced mortality near the ground favors rapid height growth and little or no branching; branching increases sharply in plants more than 50 cm tall (Fig. 3), in which fire-induced mortality is less than 4% and shows little additional decline with height. (The proportion of individuals with different numbers of branches fits a Poisson distribution for each height class ($r^2 > 0.90$), with λ increasing linearly with height x in cm ($\lambda = 0.013*$x $+ 0.042$, $r^2 = 0.97$, $P < 0.01$ for 2 d.f.)). Thick bark and massive leaf rosettes appear to insulate the cambium and terminal leaf meristems from heat damage from brief ground fires, and also select against branching and dissipation of protection resources.

Discussion

The ecological importance of fire in promoting *Neblinaria* atop Cerro de la Neblina is suggested by six facts: (i) *Neblinaria* shows high survival following fire, whereas all other woody plants found with it at the study site show no survival, (ii) lightning strikes appear common; (iii) nearly monospecific stands of *Neblinaria* dominate the drier, slightly elevated areas of large, open plateaus on the summit, even though several other woody species can grow under similar edaphic and climatic conditions (Table 1); (iv) these additional species are most common along waterways and in deep ravines that often are wetter or topographically protected from fire, and in which the tallest and apparently oldest *Neblinaria* are found as minority elements; (v) *Neblinaria* appears to be ecologically dominant only on the northwestern leeward plateaus of the horseshoe-shaped summit of Neblina (Maguire 1955; Maguire et al. 1972; establishment of twelve camps on plateaus atop Neblina during the current expedition showed that only those on the northwestern rim of Cañon Grande had large stands of *Neblinaria*), which presumably are more likely to desiccate and be prone to fire than the southeastern plateaus; and (vi) extremely infertile and non-retentive soils insure that any destruction wrought by fire would have long-lasting effects. Neblina may have favored the evolution of a fire-adapted montane species because it has extensive summit plateaus undissected by major barriers to fire (see Givnish 1981), has relatively dense vegetation compared to that on many other large tepuis, and stands as an isolated

pinnacle in a humid lowland region, likely to generate convective thunderstorms.

Many woody plants of tepui summits – including taxa possibly ancestral to *Neblinaria* in the large, widespread genus *Bonnetia* – have a growth form involving sparsely branched axes with terminal leaf rosettes (Steyermark 1966, 1967; Brewer Carias 1976). We do not wish to imply that this general growth form arose initially as an adaptation to fire. The slender branches, thin bark, relatively few leaves per rosette, and sensitivity to fire seen in several tepui shrubs with this habit argue against an origin favored by fire. Several factors other than fire, as indicated previously, can promote sparse branching and/or terminal leaf rosettes. In the rainy, excessively humid, high-elevation, frost-free environment of tepui summits, such growth forms seem more likely to be adaptive in protecting tender buds and young leaves from ultraviolet radiation (Steyermark 1966, 1967; Brewer Carias 1976) and leaching, and/or preventing a plant from being smothered by rampant lichens and bryophytes.

The growth form of *Neblinaria* is a highly unusual, previously undescribed adaptation to fire on extremely sterile substrates. Its occurrence indicates that fire in tropical forests – recently shown to be important in certain seasonal lowland areas of the Neotropics and Paleotropics (Huber et al. 1984; Sanford et al. 1985; Leighton and Wirawan 1986) – can shape plant evolution even in wet montane sites. Functionally similar grown forms, apparently favored by similar conditions of fire over sterile substrates, occur in *Vellozia* (Velloziaceae) and *Xanthorrhoea* and *Kingia* (Xanthorrhoeaceae). Fire-tolerant shrubs of *Vellozia* inhabit granitic or sandstone outcrops in the Guayana and Brazilian Shields and have sparsely, divaricately branched axes with persistent, fire-resistant leaf bases (personal observation). *Xanthorrhoea* and *Kingia* are fire resistant, unbranched treelets crowned with similar tufts of grass-like leaves, and inhabit sterile, fireswept mallee heaths and woodlands in southern Australia (Erickson et al. 1979). Additional ecological studies in the Guayana Highlands, of this is one of the first, will be required to determine whether similar growth forms in *Chimantea* (Rubiaceae), *Neogleasonia* and *Neotatea* (Theaceae) are adapted to fire or some other environmental factor.

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