Multiple Branching at Nodes of *Symingtonia populnea* (Hamamelidaceae)

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Abstract

Vertically oriented sunlit shoots on *Symingtonia populnea* trees in the mountains of Malaysia produce multiple branches at nodes. The multiple axillary branches originate as branches of the vascular trace to the primary lateral bud. Plasticity in the number of branches produced per leaf axil allows *S. populnea* considerable architectural flexibility in response to environmental heterogeneity.

Introduction

Symingtonia populnea (R. Br. ex Griff.) Steen. (Syn. *Bucklandia populnea* R. Br. ex Griff. and *Exbucklandia populnea* R. W. Brown) is an early successional tree species of upper montane ericaceous forests (100–300 m) in tropical SE. Asia. On the mountains Gunong Ulu Kali and Gunong Brinchang in Peninsular Malaysia, it is prominent along roadsides but within the forest it is restricted to large treefall gaps and landslides. We were attracted to *S. populnea* by a branching pattern that is rare among dicotyledons and possibly unique among dicotyledonous trees.

Symingtonia populnea trees continuously produce leaves (Ng, 1979) and sylleptic branches, that is, branches that develop simultaneously with subtending leaves and main shoots (Tomlinson and Gill, 1973). All axes are orthotropic with distichous leaf arrangement and lateral inflorescences. Although there is no initial morphological differentiation among branch axes, some grow more slowly than others and these become displaced further from a vertical orientation than leader shoots. Using the system proposed by Hallé and Oldeman (1970) for classifying plant architectural types, this combination of characters conforms with Attim's model. However, *S. populnea* trees diverge from this familiar growth pattern when a second and sometimes a third branch emerges from a leaf axil, especially on vigorously growing leader shoots (plate 1).

The occurrence of multiple branching at nodes appears to depend on the particular shoot's vigour and position in the crown as well as on the position of the tree relative to its neighbours. Shaded trees and shaded branches on well illuminated trees rarely produce more than one branch per node. *Symingtonia populnea* trees planted in full sun in the lowlands, well below their natural altitudinal range, manage to survive but are unhealthy; the frequency of multiple branching at nodes on these trees is extremely low.

To establish the frequency with which nodes on well illuminated leader shoots and nodes on shaded subordinate branches give rise to more than one lateral branch, we counted branches at nodes on five small (3–6 m tall) trees growing in full sun on Gunong Ulu Kali. To allow branches time to develop and to avoid the potential

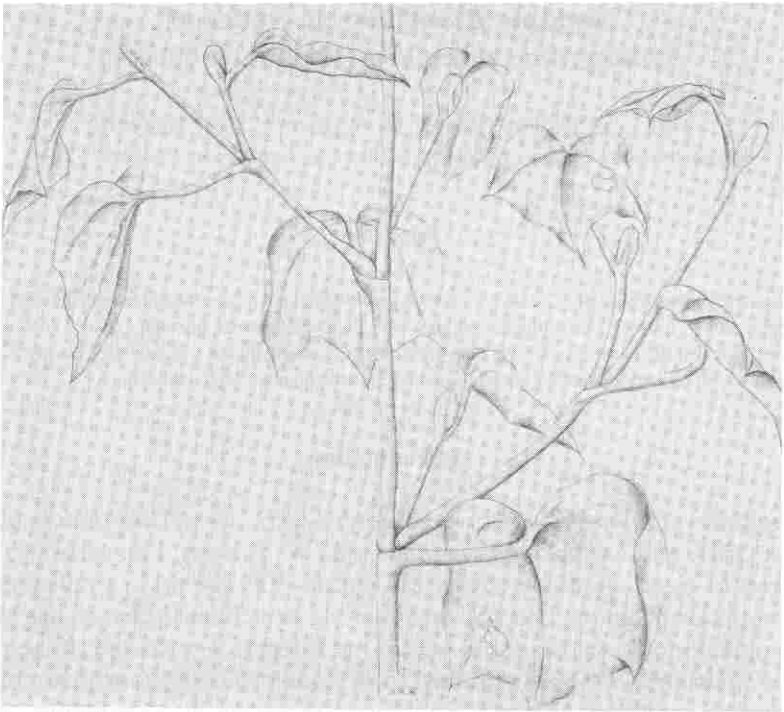

Plate 1. Pencil drawing of a *S. populnea* shoot showing development of multiple axillary branches along the main axis. (About 1/5 life-size).

problem of branch loss, neither the youngest nodes nor nodes on branches more than 3 cm diameter were included in the census. Branch departure from vertical orientation was used as a measure of vigour; overtopped branches became more horizontal with age.

On vertically oriented shoots (less than 10° from vertical), 177 of the 335 nodes examined had two branches, while on branches diverging from vertical by more than 10° only 51 of the 872 nodes examined had two branches. This difference is highly significant ($G = 441$, $P < 0.01$).

Buds on *S. populnea* trees are enveloped by pairs of large, tightly appressed, obovate, to oblong stipules (plate 2). When the stipules unfold, the enclosed main axis and at least one lateral branch are 1–3 cm long. The unique arrangement of twice-folded petioles (Lubbock, 1899) allows for this extended development within the stipules. In most cases in which a second branch develops, it does so slowly during which time one or two new leaves and branches are produced by the main axis. Sometimes the delay before emergence of the second branch is more prolonged but we have never observed newly expanded branches from axes more than 3 cm in diameter. The first branch produced at each node was smaller in diameter, had shorter internodes, and usually had smaller leaves than the main axis. Second branches at nodes are smaller than first branches. Where there was no branch loss, these size differences were further accentuated by differential growth.

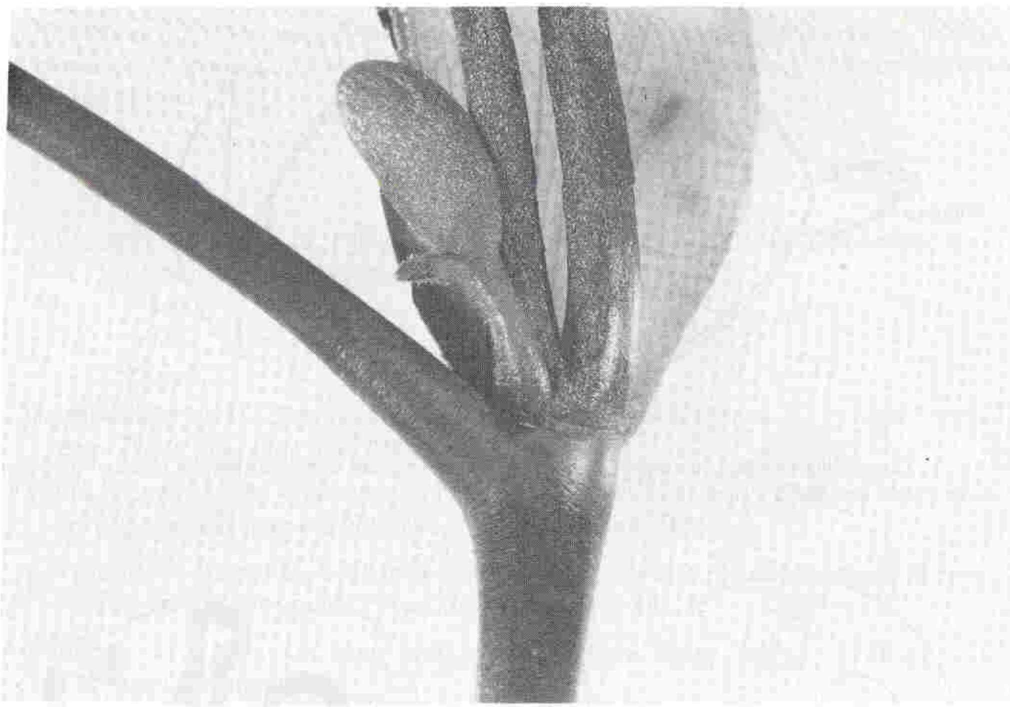

Plate 2. *S. populnea* shoot apex with one stipule removed. (Approximately life-size).

Developmental studies of *S. populnea* shoot apices revealed that multiple axillary buds originate as branches of the vascular trace to the primary lateral bud. This branching results in a proliferation of successively higher order axillary lateral meristems (a secondary bud complex; Hallé *et al.*, 1978) forming what might be called an embryonic short shoot. In *S. populnea*, each successive axillary branch bud is oriented at approximately 90° to the previous bud, forming a spiral arrangement (fig. 1). Both left-handed and right-handed spirals were observed. Up to four orders of branching were observed within a single apex, and although such "precocious" branching was not limited to apices taken from vertically oriented shoots, it was more vigorously expressed there. Prophyllary buds are known to occur in a variety of species, for example, in many bamboos (McClure, 1976), *Leptocarpus simplex* (Tomlinson, 1973), *Liquidambar styraciflua* (Kormanik and Brown, 1967), and *Gossypium* spp. (Mauney and Ball, 1959; Cook, 1911). *S. populnea* shoot apices failed to reveal any prophylls, stipules, or other organs subtending the higher order branch buds. Vascular connections, however, show that each successive branch bud (both in terms of initiation and maturation) is an offshoot of the preceding bud (fig. 2).

Plasticity in branching pattern allows *S. populnea* trees to display many leaves where conditions are favourable by responding architecturally to within-crown and within-habitat environmental heterogeneity. A similar response was observed in *Acer saccharum* in which leader shoots produce a significantly greater number of

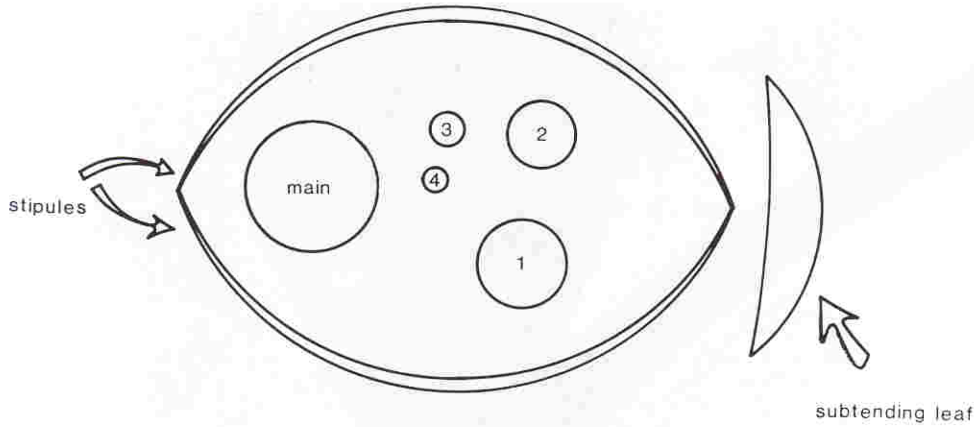

Fig. 1. Diagrammatic representation of a *S. populnea* leader shoot apex showing the terminal (main) and four axillary buds.

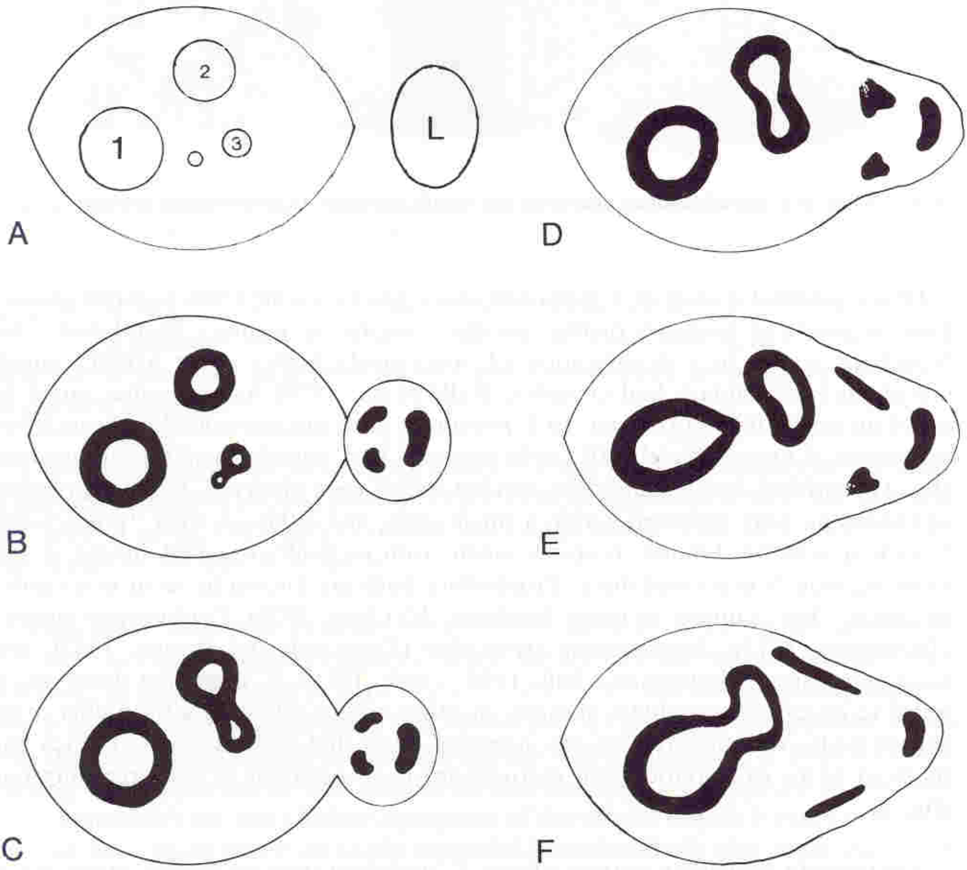

Fig. 2. Drawings of successive transverse sections of a *S. populnea* shoot apex (basipetal sequence, *A* = uppermost; solid area represents vascular tissue).

first order branches per second order branch than lower limbs (Steingraeber, 1982). However, *S. populnea* is distinctive in altering both the frequency and the pattern of branching.

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