

CAULIFLORY AND RAMIFLORY IN NEW ZEALAND PLANTS

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What is Cauliflory?

Plants have many ways of displaying their flowers to advantage, for pollination either by wind or by attracting pollinators. One of the most curious floral displays is the production of flowers or inflorescences, (and fruits) directly from the trunk; this is termed "Cauliflory", the literal meaning "stem flower". A variation of cauliflory occurs when flowers and fruits appear on woody branches directly below the leaves; this is termed "Ramiflory". Flowers are produced for several seasons from the same position on the trunk or branches.

There are two main sources from which cauliflorous and ramiflorous flower buds are produced. Some species produce adventitious buds arising endogenously, deep within existing tissue by resumed meristematic activity of living cells. The shoots formed in this process grow outward and become located in the bark of the tree.

In other species buds form in the axils of the leaves and remain alive, growing outward a little each year. The bud's growth is able to keep pace with the expansion of the trunk. Buds produced in this way usually only produce scale leaves but buds developing in their axils may also develop and extend out beside the first bud. Over time, a mass of buds is developed at the bark surface. Epicormic or cauliferous buds formed in this exogenous way are known by the term "pre-ventitious", in contrast to adventitious buds formed endogenously (Bell 1993).

The sites at which cauliflorous and ramiflorous buds are present can often be seen as swellings of the bark surface as can be observed on the branches of *Melicytus ramiflorus*.

Cauliflory and Ecology

Alfred Russel Wallace (1823 - 1913), a British naturalist, theorised that cauliflory is a condition that arose in the dark understory of the tropical forest as a result of selection for stem flowers which are more apparent to pollinators than are canopy flowers.

Indeed species displaying cauliflorous flowers are often, but not exclusively, understory trees. They are therefore growing in the shade of canopy trees and flowers are protected from heavy tropical downpours and excessive heat. As a result of the shady environment the flowers of cauliflorous species are generally larger in size than flowers of tree species

forming the canopy. This makes them more conspicuous to potential pollinators. Cauliflorous flowers are also more sturdily attached to the trunk and can support the weight of large fruits which would otherwise cause branches to snap under their weight. They are better able to withstand visits from bird and mammal pollinators and are well positioned for easy access by these animals for fruit dispersal.

The cauliflorous habit is chiefly associated with cross pollination as many species with this habit are not self fertilised. Animal visitors to cauliflorous trees include marsupial and placental mammals that climb on trunks and limbs to feed on nectar and fruits, perching birds that land on limbs to feed on fruit, pollinator and frugivore bats that cling to trunk and limbs while feeding, and small, crawling and flying insects that visit flowers below the canopy.

Cauliflory and ramiflory, being a habit originating in rainforest environments, is therefore most common in tropical regions and on trees with thin smooth bark. It is less commonly found in temperate regions and rarely occurs on trees with thick and / or stringy bark. Cauliflory and ramiflory are therefore not well represented in the New Zealand flora as we only have a very small representation of tropically derived species.

Tropical species with Cauliflorous flowers

Undoubtedly tropical species possess the most spectacular cauliflorous flowers some of which also produce very large fruit. Flowers can appear singly or in clusters, or sometimes as whole inflorescences arising directly from the trunk (Fig. 1).



Figure 1. *Saraca cauliflora*, a tropical cauliflorous species native to Malaysia. It grows in the understory along stream margins. This specimen was photographed in the Singapore Botanic Gardens. *Photo: Dean Pendrigh*

One of the best known examples would be *Theobroma cacao* from which chocolate is derived. It is an evergreen understory tree growing from 4–8 metres in height. A member of the Sterculiaceae family, it has white and pink flowers pollinated by flies in the order Diptera. The pods are 15–30 cm long and 8–10 cm diameter and when ripe weigh up to 500 grams. The jackfruit *Artocarpus heterophyllus* has the largest tree borne fruit in the world with fruit up to 90 cm long and 50 cm wide and weighing as much as 36 kg. This species is monoecious, the inflorescences arise from short stems attached either to older branches or the trunk. It is easy to see the advantage in adopting a cauliflorous habit with such heavy fruit. Other large fruited cauliflorous species include the bat-pollinated calabash, *Crescentia cujete*, with fruits to 30 cm diameter and *Averrhoa carambola* (star fruit) which have fruits 12.5 cm long and 6 cm wide.

Other species such as the Cannonball tree, *Couroupita guianensis*, produce cauliflorous inflorescences. In this species the inflorescence, which in this case is a raceme, can be up to 3 m long which gives the tree a rather messy appearance. The flowers of *C. guianensis* are up to 10 cm in diameter and fragrant at night which attracts bat pollinators. Xylocarpa bees are also attracted to the flowers. Fruits are 15 to 24 cm in diameter. Some *Ficus* species also produce large inflorescences such as *Ficus sur* from Southern Africa which when fruiting has from 10 to 100 fruit up to 4 cm in diameter, and *F. minahassae* can have inflorescences up to 3 m in length. Fruit size is much smaller but the sheer number of fruit adds up to a lot of weight!

Durio zibethinus, the durian, with fruit to 35 cm long is ramiflorous, producing flowers and fruit on branches big enough to support the weight of the fruit. *Castanospermum austral*, Moreton Bay chestnut, is also ramiflorous. The 4 cm long flowers are produced in racemes and are pollinated by lorikeets which feed on nectar. The legume (pod) is up to 30 cm long. The genus *Syzygium* has several ramiflorous species for example *Syzygium malaccense*, the Malay apple, and the Australian *Syzygium cormiflora*.

This is a sample of some of the cauliflorous and ramiflorous species found in the tropics, there are many more. Now I will describe the New Zealand examples.

Cauliflory and Ramiflory in New Zealand

As mentioned earlier New Zealand has only a small tropical component in its flora. The species have affinities with species found in Melanesia, Queensland and Malaysia. New Zealand has only one truly cauliflorous species *Dysoxylum spectabile* (kohekohe) from the family Meliaceae. It is a tropical looking tree with panicles of flowers up to 30 cm long which emerge from the trunk and larger branches. It is distributed throughout

the North Island and as far south as Nelson and the Marlborough sounds. The flowers are adapted to moth pollination but also have some features which suggest an adaptation to bird pollination eg: a sturdy waxy flower which protects the ovules from damage by bird beaks (Newstrom & Robertson 2005). Tui (*Prothemadera novaeseelandiae*), bellbirds (*Anthornis melanura*) and silvereyes (*Zosterops lateralis*) are birds known to visit these flowers. Flowers hanging from the trunk are strong enough to allow bellbirds to forage for nectar. Tui on the other hand can only gather nectar from flowers emerging from larger branches. Kereru (*Hemiphaga novaeseelandia*), weka (*Gallirallus australis*) and kokako (*Callaeas cinerea*) are known dispersers of *Dysoxylum* fruits. Other members of the genus *Dysoxylum* also have cauliflorous flowers. The genus consists of about 75 species and is found in New Guinea, New Caledonia, Australia, New Zealand and the Western Pacific.

Ramiflory is more common in New Zealand. The majority of ramiflorous species in New Zealand are represented by 2 genera, *Melicytus* in the Violaceae family, with 24 species as illustrated in Eagle's Complete Trees and Shrubs of New Zealand 2006, and *Myrsine* in the family Myrsinaceae with 12 species. The other ramiflorous species are found in the Myrtaceae with 2 species of *Metrosideros*, the Onagraceae with *Fuchsia excorticata* and the Bignoniaceae with *Tecomanthe speciosa*. All species show the ramiflorous habit clearly (Fig. 2) apart from *Myrsine nummularia* and *Melicytus micranthus* which have their flowers and fruits scattered among the leaves.

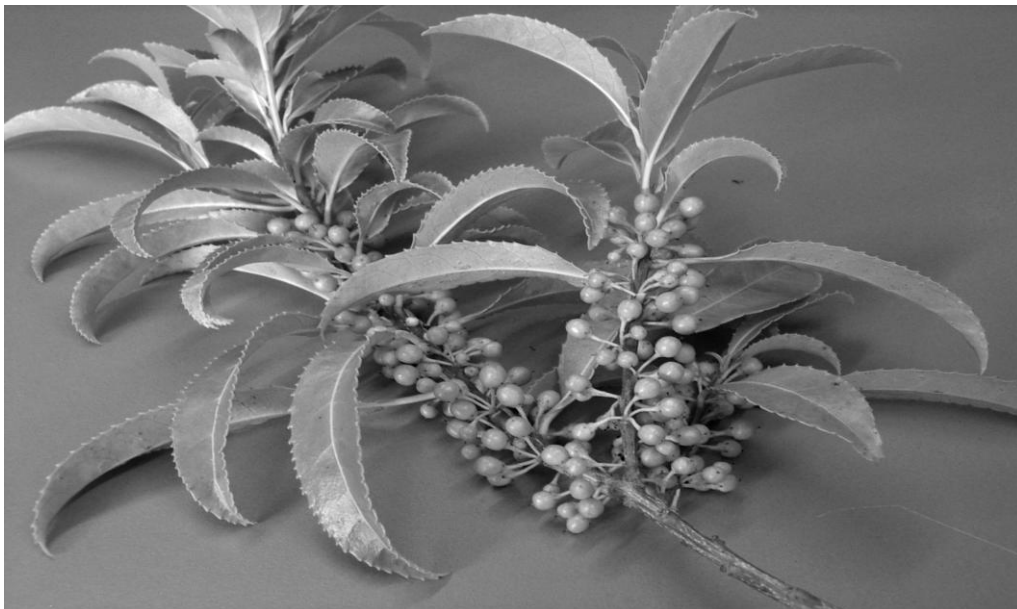


Figure 2. A fruiting branchlet of *Melicytus lanceolatus* showing fruits clustered on stem below the leaves. Photo: Dean Pendrigh

The ramiflorous habit in New Zealand is not only found in trees such as in *Melicytus ramiflorus* (Fig. 3) and *Myrsine australis* but also is a major



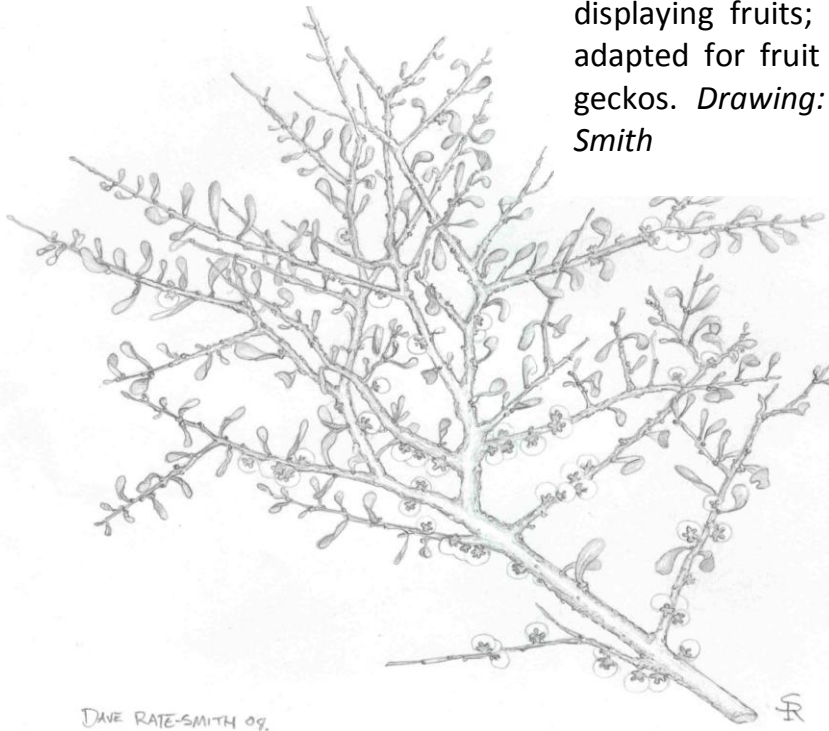
Figure 3. Ramiflorus flowers of *Melicytus ramiflorus*. Photo: Dean Pendrigh

feature of divaricating shrubs in these two genera. In the New Zealand ramiflorus species no flowers are produced in the first season's growth. Flowers will first appear in the second season after most of the leaves have fallen from the first season's growth. In the following season flowers appear from the same places that have already borne flowers previously. Flowering is only likely to occur for a few seasons. Flowering wood is usually about pencil thickness although occasionally flowers may be produced on thicker wood. I have observed flowers of *Melicytus ramiflorus* on branches up to 25 mm in diameter on a 10 year old specimen in the Christchurch Botanic Gardens. Old specimens tend to only produce flowers on 2–3 year old wood. Flowers occur in 2–10 bundled fascicles below the leaves. They are 3–4 mm diameter and appear from November to February. The fruits are purple and appear from November through to March.

Not much is known about the potential pollinators of our ramiflorus species. They are most likely pollinated by flies or small bees. Geckos and skinks are thought to be responsible for dispersal of fruits of divaricating species. Certainly *Melicytus alpinus* (Fig. 4, p. 39), with its dense tangle of branches and pendulous flowers with purple flecked white fruits, has its fruits ideally located for access by geckos and skinks (Whitaker 2008). The flowers appear in December and February while fruits occur from January well into the winter months. It is unlikely that birds are able to reach the fruits under the tangled network of branches. *Melicytus alpinus* occurs in rocky habitats where geckos and skinks occur. It is also more likely that they are the most suitable vectors to disperse the fruits to suitable micro habitats that favour the germination of this species. However, more study and observations need to be carried out on the role that geckos and skinks play in the ecology of *M. alpinus* and other divaricating shrubs in New Zealand. So far it has been difficult to prove

the effectiveness of geckos and skinks in the dispersal of fruits of our divaricating plants.

Figure 4. *Melicytus alpinus* displaying fruits; a plant well adapted for fruit dispersal by geckos. Drawing: Dave Rate-Smith



Species of *Myrsine* are either small trees such as mapou, *Myrsine australis*, or *M. salicina* which grow 6–8 m high, or divaricating shrubs such as *M. divaricata* and *M. argentea*. Both *M. australis* and *M. salicina* have flowers in dense fascicles located on bare stems below the leaves. *Myrsine australis* is commonly found throughout New Zealand in coastal to montane forests and *M. salicina* is found mainly in the North Island and milder western areas of the South Island. The divaricating species have their flowers scattered along the branches, usually protected beneath the outer most branchlets.

The only two ramiflorous *Metrosideros* in New Zealand, *M. diffusa* and *M. parkinsonii*, are both climbers. *Metrosideros diffusa* is distributed throughout North, South and Stewart Islands. It can grow up to 6 m tall, the white flowers occurring on the stems just beneath the leaves. *Metrosideros parkinsonii* can grow to a similar height but is of limited distribution being found only on Great Barrier Island, in NW Nelson and near Westport. Its flowers are red and in compact cymes below the leaves. Both species are in the subgenus *Mearnsia* with close relatives in New Caledonia. Other ramiflorous species of *Metrosideros* occur elsewhere such as *M. scandens* and *M. ramiflorus* in Papua New Guinea.

Fuchsia excorticata has flowers which appear in no particular order on young and old branches. They are usually single but can occur in small clusters scattered over the branches. *Fuchsia excorticata* is gynodioecious, that is both female and perfect flowers occur on the same plant. The flowers are visited by bellbirds and tui which collect nectar and pollinate the flowers. Fruits are a dark purple to black berry to 10 mm long and are bird dispersed being a favourite fruit of the kereru.

Tecomanthe speciosa is a woody liana restricted to the Three Kings Islands. It produces creamy green flowers above the axils of leaf scars on the older wood. They are up to 3.5 cm long in clusters of up to 30. This is a tropical looking species. One of only about 5 species in the genus, its relatives are found in Eastern Queensland, New Guinea and the Solomon Islands. There are 2 specimens of *T. speciosa* in the Christchurch Botanic Gardens, one in the Fern House and the other outside on the north facing wall of the Fern House. However, they have never produced flowers. There is also a specimen of *Tecomanthe dendrophylla*, a species native to New Guinea and the Solomon Islands, displayed in Cunningham House in the Christchurch Botanic Gardens. This species has pink and white flowers to 11 cm long which appear on the old wood.

If one stretches the definition of ramiflory, species such as *Pseudowintera axillaris* and *P. colorata* (Salmon 1985 pp. 100–102) and *Geniostoma ruprestre* var. *ligustrifolium* (Salmon 1985 p.292) could be included. Although not truly ramiflorous they have flowers that are grouped in fascicles or are solitary in the axils of the leaves. Sometimes the flowers appear well down the stem beneath the leaves thus appearing ramiflorous. On close examination it can be determined that they are arising from the axils of old leaves. In truly ramiflorous species all signs of old leaf scars are gone; usually they have long been engulfed by the expanding bark of the tree or by the expansion of preventitious buds.

Vitex lucens may occasionally produce one or two flowers from older wood and so appear to be ramiflorous but the flowers are usually produced in the axils of the leaves.

Dawson (1988) p. 35 notes *Pennantia baylisiana* from the Three Kings Island as being cauliflorous. Inflorescences are more often in terminal panicles with often one or two panicles appearing below the leaves (Metcalf 1991 p. 247).

Plants with Cauliflorous flowers

Family – Meliaceae

Dysoxylum spectabile in Eagle (2006) pp.466–477, Dawson (1988) p.34, Salmon (1985) p.241

Plants with Ramiflorus flowers

Family – Violaceae

Melicytus alpinus which also includes 7 unnamed taxa as illustrated in Eagle (2006) pp.116–127

Melicytus chathamicus in Eagle (2006) pp.116–117

Melicytus crassifolius plus 1 unnamed taxon in Eagle (2006) pp.114–117

Melicytus drucei in Eagle (2006) pp.114–115

Melicytus flexuosus in Eagle (2006) pp. 126–127

Melicytus lanceolatus in Eagle (2006) pp.102–103, Salmon (1985) pp.115–117

Melicytus macrophyllus in Eagle (2006) pp.100–101, Salmon (1985) p.120

Melicytus micranthus in Eagle (2006) pp.104–105

Melicytus novae-zealandiae in Eagle (2006) pp.106–107, plus 1 unnamed taxon in Eagle (2006) pp.112–113

Melicytus obovatus and 3 unnamed taxa in Eagle (2006) pp.106–113

Melicytus ramiflorus in Salmon (1985) pp.118–119, Eagle (2006) pp.98–99, and 1 unnamed species from the Three Kings Islands and Northland, in Eagle (2006) pp.96–97

Family – Onagraceae

Fuchsia excorticata in Eagle (2006) pp.140–141, Salmon (1985) p.122, Dawson (1988)

Family – Myrsinaceae

Myrsine argentea in Eagle (2006) pp. 630–631

Myrsine aquilonia in Eagle (2006) pp. 630–631

Myrsine australis in Eagle (2006) pp. 620–621

Myrsine chathamica in Eagle (2006) pp. 622–623

Myrsine coxii in Eagle (2006) pp.624–625

Myrsine divaricata plus 1 unnamed taxa in Eagle (2006) pp.626–629

Myrsine oliveri in Eagle (2006) pp. 624–625

Myrsine kermadecensis in Eagle (2006) pp. 622–623

Myrsine nummularia weakly ramiflorus. Flowers produced between leaves. In Eagle (2006) pp. 632–633

Myrsine salicina in Eagle (2006) pp.618–619

Myrsine umbricola in Eagle (2006) pp. 632–633

Family – Myrtaceae

Metrosideros parkinsonii in Dawson (1988) p.35, Simpson (2005) p.48–49, Eagle (2006) pp. 248–249, Salmon (1985) p. 160

Metrosideros diffusa in Eagle (2006) pp. 256–257

Family - Bignoniaceae

Tecomanthe speciosa in Dawson (1988) p.35, Moore & Irwin (1978) p.158, Eagle (2006) pp.1046–1047

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