

Contents

1. Introduction: the leaf and the pressures it faces	1
Herbivory and the terrestrial carbon cycle	2
The range of leaf-eating organisms to be considered	4
Herbivores outnumber plants	5
Vertebrate folivores	11
The nature of the leaf	17
Summary	26
2. Leaf colour patterning and leaf form	29
The palette of colour available to leaves	29
Folivore exposure colouration	31
Non-deceptive colouration: warning	33
Deceptive colouration: colonization and damage mimicry	37
Dissimulation and crypsis	40
Crypsis through movement	44
3. Structural defences and specialized defence cells	47
Leaf surface defence cells and leaf surface habitats	47
Stings	52
Glochids, hairs, prickles, and thorns	55
Silica: targeting teeth and mandibles	62
Crystalline defences	65
Fibre cells and sclereids	68
Defence cells: idioblasts	70
Exudates	70
Summary	73
4. Chemical defences	75
Selection for novel defence chemistries	75
Alkaloids	86
Phenolics	92
Detoxification: the important tail end of the defence process	100
Terpenes	104
5. Inducible defences and the jasmonate pathway	115
Inducible proteins that deplete energy and essential nutrients	115
The moving defence horizon	119
Activating inducible defence: the importance of having good teeth	120
The jasmonate pathway	122
Jasmonate and growth	132

viii Contents

The evolution of jasmonic acid-based signalling	135
The suppression of jasmonate signalling by herbivores	138
6. Top-down pressures and indirect defences	141
Plant population remodelling after carnivore removal	141
Ant-plant interactions, extrafloral nectaries, and food bodies	143
Mite domatia	147
Predator and parasitoid attraction by plant volatiles	150
Kudus and acacias: a cautionary tale	154
7. Release and escape from herbivory	155
Release from herbivory: anachronistic defences	155
Escape from vertebrate folivores	161
8. Escape in space: the cliff trees of Socotra	165
The cliff trees of Socotra	165
Candidate invertebrate herbivores on Socotra	172
Candidate vertebrate herbivores on Socotra	172
Synthesis	177
Wealth and social context	177
Tolerance and escape	177
Defence expenditure is proportional to attack pressure	178
The time factor in defence	178
Energetics: leaves and digestive tracts have co-evolved	178
Defence inducibility and the jasmonate pathway	179
There is no single best defence strategy	179
Leaves co-operate with the enemies of their enemies	180
Relevance of plant defences in agriculture and industry	180
Glossary	183
References	187
Index	205