Nocturnal petal movements in the Asteraceae

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ABSTRACT

Nocturnal petal movements were recorded from 48 genera and 106 species growing in cultivation at the Royal Botanic Gardens, Kew and in the wild in Canada, Great Britain, France, Italy, Greece, Canary Islands and South Africa. Seven different night positions of petals, as distinct from day positions, are recognized and discussed.

RÉSUMÉ

LES MOUVEMENTS NOCTURNES DES PÉTALES DES ASTÉRACÉES

Des mouvements nocturnes des pétales ont été observés dans 48 genres et 106 espèces croissant en culture dans les Jardins Botaniques Royaux de Kew et en pleine nature au Canada, en Grande Bretagne, France, Italie, Grèce, aux Iles Canaries et en Afrique du Sud. Sept positions nocturnes différentes des pétales, distinctes des positions diurnes, sont reconnues et discutées.

INTRODUCTION

One of the great differences between plants and animals is that animals are mostly mobile, whereas plants are essentially static organisms. When plants do move, the movements are usually restricted to a particular organ or group of organs. Such movements are usually subtle and slow, or rapid and unexpected. It is these two qualities of plant movements that have fascinated naturalists for hundreds of years and, as this paper is evidence, continue to do so today.

Although the study of flower movements, or anthokinetics, as some prefer to call it (Goldsmith & Hafenrichter, 1932), has been carried out by amateur naturalists and professionals alike, little attention has been given to the phylogenetic significance of such movements. Such studies have established the variability and frequency of movements of flowers and flower parts, but have scarcely considered their ecological importance or their evolutionary and adaptive significance.

Such ideas were very far from my mind when I made my first observations on petal movements in the Asteraceae. The earliest observations were merely visual impressions, but ones which gradually coalesced into discernible phenomena. It became clear to me that the asteraceous capitulum is a complex structure with many interacting functions and that a cursory inspection of any single component is fraught with pitfalls if generalizations are to be drawn from data gathered about them.

This can be seen very clearly in the work of Leppik (1977). According to Leppik the most attractive floral patterns and specialized pollination mechanisms in the Asteraceae have co-evolved with the sensory development of their pollinators. However, as Burtt (1975, 1977) has so clearly noted, the structure of the capitulum has to meet the demands of both the flowering and the fruiting phases, and not, as Leppik (1977) suggests, the flowering state only.

It seems clear that if we are to understand the adaptive significance of structures and their functions, we need to view the flower and inflorescence/infructescence as evolutionary compromises between inherent genetic constraints and those constraints acting from outside the plant (Polhill, Raven & Stirton, 1981). This requires a closer look at the complex relationships that occur between component parts, how these change in position and function during their different developmental stages and how during such development they may combine in different sequences.

The study of floral movements in the Asteraceae has already provided fascinating information, for example, irritability of the pollen-presentation mechanism (Small, 1919), and involucral movements (Burtt, 1977). The present study continues in this tradition and, although a long-term study is needed before generalizations can be drawn of the type discussed above, enough data has been collected to warrant a preliminary descriptive report.

MATERIAL AND METHODS

Data were recorded from plants growing both in the wild and in cultivation. Notes were made of the position of petals one hour before sunrise, six hours after sunrise, just before sunset and finally, one hour after sunset. The majority of the species studied were growing in open cultivation in order-beds at the Royal Botanic Gardens, Kew, and were observed in two different summers, 1978 and 1979. The remaining observations were made on plants growing in the wild in Canada, Great Britain, France, Switzerland, Italy, Greece, the Canary Islands and in southern Africa. Only the movements of ligulate florets were recorded, and care was taken to avoid older flowers as in these some petals begin to adopt senescent positions which are often quite different from the night positions.

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RESULTS

The movement of ligulate florets towards their night position begins just before or just after sunset and may take one quarter of an hour to three hours to complete. Likewise, their return to the daylight position occurs predominantly after sunrise, often as late as mid-morning.

Although seven different night positions have been found (Fig. 1.1–1.7) and figured, I have also seen three others, two of which occur in *Gazania*. In some species the individual petals remain horizontal or rise somewhat vertically as in Position 3 but, instead of remaining flat, the petal margins roll either inwards or outwards (Fig. 1.8). Finally, I recall seeing an endemic daisy in the Canary Islands, in which the petals rolled upwards until they rested on top of the capitulum (Fig. 1.9), that is, the opposite of Position 1.
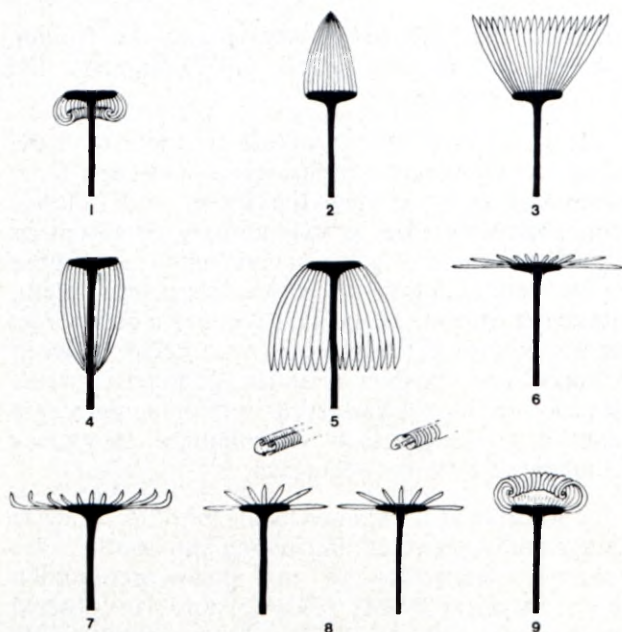

FIG. 1.—Nine basic night positions of ligulate petals in capitula of Asteraceae.

The three commonest night positions are numbers 1, 2, 4 and 5 respectively (Table 1.). Position 2 is significantly more widespread than any other position and occurs in the tribes Anthemideae, Arctoteae, Astereae, Inuleae and Lactuceae. Some tribes appear to be charaterized by a single position, for example, position 2 in the Lactuceae, Arctoteae, Cynareae and Calenduleae, whereas in other tribes such as the Anthemideae and the Heliantheae three to five positions may be adopted.

Broadly speaking, each genus appears to have a definite and characteristic night position. Exceptions are *Argyranthemum*, *Chrysanthemum* and *Erigeron* which all have two types of night positions. No species have been found which adopts more than one night position.

DISCUSSION AND CONCLUSIONS

The involucre is perhaps the most important organ of the capitulum that moves in response to internal and external stimuli. Burtt (1977) lists five functions of the involucre which, if considered ecologically, all involve anthokinesis. These include the protection of young flowers, the protection of mature flowers at night or during inclement weather, the attraction of pollinators, the protection of developing fruits, and the release of ripe achenes, or their enclosure and dispersal as a unit.

The second most obvious organ that is anthokinetic is the corolla. As we have seen these movements are most pronounced in ligulate corollas. Although these are often synchronous with involucral movements, they usually occur at night or during the day under certain environmental conditions. It is perhaps significant that those capitula which have weakly developed involucres are often protected by the shift of the protective role from the involucre to the enlarged outer ligulate corollas. For example, in *Gazania* the involucre is robust and dominates opening and tight closure of the flowers, whereas in some of the Calenduleae the petal movements are more dominant. Ligulate petals also help in the attraction of pollinators, in their own right, or by exposing or camouflaging the UV-absorbent disc florets. Such day-time movements may have parallels with the night movements. Is it possible that Positions 3, 6, 7 may be involved with moth visitation?

A dominant feature of many Asteraceae are their brightly coloured flowers often of intense yellow and orange hues. Is it possible that the ligulate florets of these colours are warning devices against herbivores and not as is generally accepted, attractants for pollinators? Can they be a combination of both? And what about the deep purpling often present on the undersurface? Does this assist in camouflage when the flower is closed? Has it a protective role in preventing damage by UV-radiation? Involucres may also be brightly coloured and/or deeply purple on their outer surfaces and so have similar attractive and/or protective roles.

These few observations and comparisons between the involucre and ligulate florets suggest that only careful observations that discriminate how and what functions are shifted from one organ to another will be useful in drawing generalizations of biological significance.

Differences between the day and night positions of ligulate florets strongly suggest that the day positions are related more closely to herbivore avoidance, pollinator attraction and protection against inclement weather. The common phenomenon of sun-tracking, considered together with the dusk and dawn movements, strongly implicate light and temperature as prime causal stimuli. Baagoe (1977) has remarked particularly on the constant occurrence of highly specialized ligule epidermis types within different taxa and suggests that they must be 'genetically fixed functional adaptations rather than ontogenetically developed structural eventualities'. Her data is fully supported by Kay, Daoud & Stirton (1981) and Stirton (1981). Although it is still too early to draw any conclusions about the possible correlation of floral movements and the microstructure of floral parts, there does

TABLE 1.—Distribution of different night positions of petals in ligulate florets of Asteraceae according to tribes and genera

Tribes / Genera	Number of species found with each type of movement							Number of species
	1	2	3	4	5	6	7	
1. Anthemideae								
Achillea			2					
Anacyclus		1						
Anthemis				3				
Argyranthemum				4	1			
Chrysanthemum				8		2		
Leucanthemum				2				
Ursinia		1						24
2. Arctoteae								
Arctotis		1						
Berkheya		1						2
3. Arniceae								
Arnica					1			1
4. Astereae								
Amellus	1							
Aster		2						
Bellis		1						
Brachycome	1							
Calotes	1							
Chareis	1							
Erigeron	2	2						
Grindelia		2						13
5. Calenduleae								
Calendula		3						
Dimorphotheca		2						
Osteospermum		1						6
6. Cynareae								
Carduus		1						
Centaurea		1						2
7. Heliantheae								
Bidens						1		
Coreopsis					3			
Helenium					2			
Helianthella					1			
Sanvitalia					1			
Tridax					1			
Verbesina							1	10
8. Inuleae								
Helipterum		3						3
9. Lactuceae								
Andryala		1						
Cichorium		2						
Crepis		5						
Hedypnois		1						
Hieracium		9						
Hyoseris		1						
Hypochoeris		1						
Lactuca		4						
Leontodon		2						
Picris		2						
Scolymus		1						
Tolpis		2						
Tragopogon		1						
Urospermum		2						34
10. Mutiseae								
Perezia	1							1
11. Senecioneae								
Ligularia	7							
Senecio					2			9
12. Tageteae								
Tagetes					1			1
TOTALS	14	56	2	17	13	3	1	106
48 genera								

seem to be ground for further investigation, particularly with respect to diurnal movements, not recorded here, but which are essentially the same as nocturnal movements and usually correlated to low periods of pollinator foraging. The possibility that those daisies which remain open at night could be moth pollinated should similarly be investigated.

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