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Achene dispersal in Asteraceae with specific reference to British and Irish *Centaurea*

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Abstract

This minireview addresses aspects of achene dispersal in Asteraceae with special reference to the genus *Centaurea* L. It was motivated by a detailed taxonomic study of *Centaurea* in the Natural History Museum British & Irish Herbarium (**BM**) as well as field observations.

Keywords: Knapweed; phyllary; achene; elaiosome; pappus

Introduction: form and function in *Centaurea*

Anyone familiar with determining British or Irish *Centaurea* in the field will know that the problem is largely one of examining phyllary morphology and overlap. On this basis it is possible, at least in principle, to distinguish *Centaurea nigra* L., *C. debeauxii* Gren. & Godr. (Fig. 1) and *C. jacea* L. and to some extent hybrids between the three which can form a hybrid swarm and may be referred to as the *C. nigra* group. A phyllary of *Centaurea* consists of a proximal portion (sometimes referred to as the phyllary proper) and a distal appendage (Fig. 1). The appendage consists of a central disc the margin of which may be more-or-less entire or divided into finger-like projections, depending on species (the disc being more-or-less entire or squamose in *C. jacea*). The older descriptions depict a gradation from a comblike array of finger-like projections, or pectinations, to finer more hairlike projections or fimbriae; including pectinations bearing fimbriae (pectinato-fimbriate) but the terms 'pectinate' and 'fimbriate' are often used interchangeably in a loose sense. The degree to which the margin of the appendage is divided or pectinated/fimbriated and the degree to which the fimbriae overlap are important diagnostic features (Marsden-Jones & Turrill, 1954; Harris, 2017).

The phyllaries (including their appendages) are generally considered the most reliable diagnostic feature for disentangling this difficult hybrid swarm (Marsden-Jones & Turrill, 1954; Harris 2017) and potentially other *Centaurea* hybrid swarms (e.g. Koutecký *et al.*, 2011; Vonica & Cantor, 2011). Early descriptions also noted the degree to which phyllaries would recurve or bend away from the capitulum; this arching away from the capitulum being strongest in the appendages (Fig. 1).

Figure 1. *Centaurea debeauxii*, Queendown Warren, 27 Aug 2017. This species is characterised by phyllaries with narrow appendages and fimbriae which (on the third row from the base of the spiral) frequently touch or partially overlap those on neighbouring phyllaries but neither overlap the neighbouring appendage disc nor cover the phyllaries completely as in *C. nigra* (Harris, 2017). Note that the appendages are strongly recurved in this specimen

Phyllary morphology is considered reliable for determining both fresh and especially dried herbarium specimens (Marsden-Jones & Turrill, 1954; Harris, 2017). A quote from Marsden-Jones & Turrill (1954) reads:

"We should like to emphasize here the value of herbarium methods. Since we can scarcely be accused of being merely herbarium botanists our remarks may have special validity. ... It is surprising how many characters can be scored with full accuracy with well prepared dried specimens."

Another distinguishing character is the pappus: absent in *C. jacea* and usually present in *C. nigra* and *C. debeauxii*, but very short in the latter two species. Individuals with an intermediate or irregular pappus have been considered to be probable hybrids (Marsden-Jones & Turrill, 1954). The pappus is also variable among certain other *Centuarea* species found in the British Isles, including casual aliens.

Determination becomes particularly difficult when all three species of the *C. nigra* group are included in hybrid swarms. Whilst studying collections of the *C. nigra* group at the NHM British & Irish Herbarium (**BM**) as part of a project to try and disentangle this hybrid swarm, obvious questions arose which will be addressed in this minireview: Is recurving of the phyllaries of any taxonomic importance? What is the function of the phyllaries? Why do some forms have no pappus? What is the function, if any, of a very short pappus? This led to a literature search on achene (cypsella) dispersal in *Centaurea* which resulted in an interesting story about form, function, ecology and dispersal. This mini-review looks at dispersal in *Centaurea*, with emphasis on British & Irish species, including casual aliens. This topic is important not just in understanding the morphology that confronts the field and herbarium botanist attempting to determine this difficult group, but also impacts on ecology and the problem of invasive species.

The achenes of some *Centaurea* species are also equipped with an elaiosome which possibly has a role in achene dispersal (discussed below). Table 1 lists the species native and alien to the British Isles, those for which published data are available are considered in this review, and details which species possess a pappus and/or elaiosome. Table 2 provides some background on the distribution of the alien species. The dispersal mechanisms and dispersal ecology of these species will form the main basis of this review where data are available. This turns out to be a rather interesting story. This review attempts to answer the questions raised above by first considering the importance of hygroscopic movements and the functions of phyllaries and the pappus. Other dispersal mechanisms and their ecological importance are then discussed. Finally, any remaining questions for future consideration are highlighted.

Achene dispersal: the importance of hygroscopic movements

The role played by the phyllary scales in achene dispersal in Asteraceae was studied by Sheldon & Burrows (1973). They used *Taraxacum* (Dandelion) as an example in which the phyllaries close up (appress to the involucre) in humid conditions and open outwards when dry, though similar hygroscopic movements can be readily observed in the *C. nigra* group (Figs. 1 to 4). Such movements are, however, much more obvious in *C. scabiosa*, in which the phyllaries will open when dry into a cup-shape or even opening right out to a flat platform (i.e. opening to between about 50 and 90 degrees from the vertical as can be readily demonstrated) allowing easy dispersal of the achenes by the slightest breeze. They will close again when moistened or in high humidity.

Table 1. Dispersal apparatus of achenes of *Centaurea* (*s.l.*) species commonly found in the British Isles

		Pappus	Elaiosome[1]	Source
C. aspera L.	Rough Star-thistle	+	?	Jana & Mukherjee (2014)
C. calcitrapa L.	Red Star-thistle	–	–	Viegi *et al.* (2003)
C. cineraria L.	Velvet Centaurea	+	+(L)	Viegi *et al.* (2003)
C. cyanus L.	Cornflower	+	+(L)	Viegi *et al.* (2003) Mukherjee (2000)
C. debeauxii Godr. & Gren.	Slender Knapweed	+	+(L+P)	Viegi *et al.* (2003)
C. diluta Aiton	Lesser Star-thistle			
C. jacea L.	Brown Knapweed	+ / –	+(P/L+P) / –	Viegi *et al.* (2003)
C. macrocephala Muss. Puschk. ex Willd.	Yellow Centaurea	+	+ / –	Mukherjee (2000) Meyer (2017)
C. melitensis L.	Maltese Star-thistle	+	+(L)	Viegi *et al.* (2003)
C. montana L.	Perennial Cornflower	+	?	Flora of North America
C. nigra L.	Common Knapweed	+ / –	+ / –	Meyer (2017)
C. scabiosa L.	Greater Knapweed	+ / –	+ (L+P)	Viegi *et al.* (2003)
C. solstitialis L. (inner achenes)	Yellow Star-thistle	+	+(L+P+S)	Viegi *et al.* (2003)
C. solstitialis L. (outer achenes)		–	–	Viegi *et al.* (2003)

[1] The basic nutrient(s) of the elaiosome: L = lipid, P = protein and S = starch.

Table 2. Species of *Centaurea* alien to the British Isles (see Clement & Foster, 1994)

C. aspera	Naturalised in the Channel Islands, casual elsewhere: https://www.brc.ac.uk/plantatlas/plant/centaurea-aspera
C. calcitrapa	Birdseed, grain, Lucerne seed, esparto and wool alien; native to the Mediterranean
C. cineraria	Garden-escape, birdseed alien; native of Sicily and Italy; sea-cliffs in southwestern England
C. cyanus (*Cyanus segetum*)	Archaeophyte; birdseed-alien and garden escape
C. diluta	Birdseed, grain and wool alien; native of southwestern Spain, northwest Africa and the Atlantic islands
C. jacea	Introduced; now much declined in the British Isles
C. macrocephala	Garden escape; naturalised on waste and rough ground
C. melitensis	Grain, wool, linseed, bird seed and esparto alien; native to the Mediterranean
C. montana (Cyanus montana)	Garden escape; naturalised on roadsides and railway banks and waste places
C. solstitialis	Birdseed, grain, Lucerne seed and wool alien; native of the Mediterranean; quite widespread in the British Isles but declining

These movements ensure that the capitulum is closed tightly in humid conditions. Sheldon & Burrows (1973) suggest that this serves to protect the pappus hairs of *Taraxacum* from entanglement and damage from falling rain drops. The achene fruit will then disperse under more suitable and drier conditions when opening of the phyllaries loosens the achenes in the capitulum and the achenes disperse with the slightest breeze.

The degree of opening and arching backwards of the recurved or reflexed phyllary appendages was used as a descriptive character in early descriptions, for example in '*Centaurea nemoralis* var. *microptilon*' mihi (Britton, 1922; note *C. nemoralis* = *C. debeauxii*) the phyllaries were described as 'not appressed' and the lower appendages as 'spreading' and this was noted as a possible morphometric character (Harris, 2017). The curving outwards of the appendages in this variety is recorded as being especially obvious in 'dry weather' as noted by 'C.L.' on an herbarium sheet (1921, specimen collected in 1920 from Graffham, v.c.13, West Sussex). This is the same signing as 'C.C.L.' on some herbarium sheets and is almost certainly a note by the botanist Charles Carmichael Lacaita (1853-1933) who described a number of *Centaurea* forms (see IPNI). He also states that this is the most common form by roadsides in West Sussex. The official description of this form includes: "Before expansion, appendages not appressed, mostly subulate or linear-lanceolate, elongated, the upper part curved outwards, the lowest appendages spreading. The greenish or arachnoid phyllaries are conspicuous, and the arched character of the appendages is most noticeable before the expansion of the capitulum." (Britton, 1922, p.414). Apparently, this form has a particular tendency to arch its phyllaries back when they open. However, one would ideally ensure equivalent conditions of ambient humidity before making any taxonomic conclusions regarding degree or nature of phyllary opening. As a further example, *Flora Europaea* (Tutin *et al*., 1976) describes the appendages of *C. jacea* as 'appressed'.

Marsden-Jones & Turrill (1954) reported these '*microptilon*' forms from hybrid swarms in the Woodstock district of Oxford: populations mostly of *C. debeauxii* with *C. nigra* introgression (and, at the time considerable introgression from *C. jacea*). The 1920 specimen from West Sussex in BM was determined as *C. debeauxii* x *C. nigra*, based on phyllary shape and overlap, with strong *C. debeauxii* characters.

In those Asteraceae in which the pappus is reduced or absent, vibration of the flowering stalk may dislodge achenes. A pertinent question is whether forms lacking a pappus need dry conditions for optimum dispersal. What is the function of phyllary movements in *C. nigra* and *C. debeauxii* with their short pappi? A typical achene of *C. debeauxii* is illustrated by Viegi *et al*. (2003) with its short pappus which seems too short to be of much use in wind dispersal (or in movement along the ground, see 'walking upwind with the pappus' below). Indeed, Marsden-Jones & Turrill stated regarding the *C. jacea* / *C. nigra* / *C. debeauxii* group: 'Even the best developed pappus in our knapweeds of this group can have little or no use as a mechanism for fruit dispersal.' Perhaps, however, they facilitate attachment to fur and feathers for animal dispersal. Indeed, Römermann *et al*. (2005) have demonstrated that this pappus type is almost as effective as hooks in attaching to animal coats (demonstrated in *Centaurea stoebe* L.) which has a similarly short pappus.

Observations of seed dispersal in our native *Centaurea* shed more light on the matter. Achenes of *C. scabiosa* have well-developed pappi and exhibit very pronounced hygroscopic movements of the phyllaries. In dry conditions both the phyllaries and pappi open wide. The phyllaries open out to form a flat platform if conditions are dry enough, or a broad open cup in intermediate conditions, and the slightest breeze will scatter the achenes. The receptacle scales are fine deciduous filaments that also blow away easily and perhaps they help catch the wind to dislodge the mass of achenes. The phyllaries close again in high humidity and will continue these movements long after the last achene has dispersed.

In contrast, in *C. debeauxii* the phyllaries open to a smaller degree and the pappi are generally poorly developed. The phyllaries in this species also open in dry conditions and close in high humidity, or when moistened, as can be easily demonstrated (Figs. 2-4). The apical phyllaries lack fimbriae or pectinations and open enough to form an apical 'pore' or 'mouth' that allows the achenes to scatter readily whenever the capitulum is gently shaken (pectinations might possibly cause too much obstruction if present on phyllaries around the capitulum mouth). When the phyllaries close they force the apical pore shut preventing achene dispersal. The receptacle scales are thick filaments that remain firmly attached to form a thick felt-like carpet covering the bottom of the whole chamber formed by the flask-like involucre of phyllaries and seem to function in keeping dislodged achenes held in the upper part of the chamber near to the apical exit. A few shakes and dislodged achenes can be seen massed near the exit and are gradually shed one-by-one upon gentle shaking. Thus, it would seem as if in the latter they are better suited to dislodging by animal activity as well as wind flexing the stems. Perhaps the short pappi, when present, assist attachment to animal fur. Clearly, a well-developed pappus would be a hindrance to such a 'shaker' mechanism. The receptacle scales also rapidly wick away any drop of water that lands on them, as can easily be demonstrated, draining the water out at the bottom between the phyllary scales, thus keeping the achenes relatively dry.

It has been suggested that the pappus of *Asteraceae* may function in helping to attach the achene to the soil Viegi *et al.*, 2003. The achenes of *Centaurea* produce no mucilage, as do the achenes of certain other *Asteraceae* (as noted by Viegi *et al.*, 2003). It has been suggested that mucilage functions to attach seeds/fruits to soil (e.g. Sun *et al.*, 2012) and to hydrate the achene prior to germination in arid environments (Yang *et al.*, 2011 in *Artemisia*) or to attach the diaspora to animal fur (see review by Small, 1918b).

Achene hairs, in those forms that have them, possibly also help in attachment to soil. The achenes of *C. cyanus* are covered in unicellular hairs (Mukherjee, 2000). The achenes of the *C. nigra* group are also covered in fine hairs and in *C. debeauxii* water-dispersal has been noted as the chief means of dispersal in populations in the USA where the achenes are described as being more hairy than in other *Centaurea* (https://wric.ucdavis.edu/information/natural%20areas/wr_C/Centaurea_debeauxii.pdf). If the hairs are hydrophobic then they possibly assist with flotation by preventing wetting of the achene surface. (It should be noted that the form categorised as *C. debeauxii* in the USA is generally considered to be a nothospecies hybrid between *C. jacea* x *C. nigra* (= *C.* x *moncktonii*) (http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=250068128) and so is not likely to be the same form referred to as *C. debeauxii* in the British Isles). Hairs may also lower the rate of descent of an achene and aid wind dispersal, if not as effectively as a pappus (Sheldon & Burrows, 1973).

Dispersal in Asteraceae is also assisted by hygroscopic movements of the pappus bristles as reviewed by Sheldon & Burrows (1973). This can be easily seen in *C. scabiosa*. In some Asteraceae, e.g. *Lactuca*, there is an annular pulvinus where the pappus filaments (setae) join the achene body and this pulvinus acts as a hygroscopic 'muscle' opening the pappus in dry conditions. This opening or spreading of the pappus is assumed to help dislodge the achenes from the capitulum and also to increase the surface area exposed to wind to increase odds of wind dislodging them. In *Cirsium* each pappus filament has its own basal pulvinus, while in *Tussilago* unequal thickening of the pappus filaments themselves causes them to bend in high humidity (these filaments are fused at their bases into an annular membrane in *Tussilago*).

Figure 2. Capitula of *Centaurea debeauxii x C. nigra* (v.c.-15, Milton Regis) – the involucres were closed when collected in humid conditions but have opened upon drying indoors. In this specimen the phyllaries remain mostly straight when open, recurving little. In some *C. debeauxii* specimens, recurving of the open phyllaries is much more pronounced (Fig. 1). This specimen is close to *C. nigra* but is from a population of hybrids ranging from more *debauxii*-like to more *nigra*-like. This plant was flowering on 27 July

Figure 3. The same specimen as in Fig. 2 after being moistened and placed in a petri-dish with damp filter paper for one hour: note that the phyllaries have almost finished closing

Figure 4. The same specimen as in Fig. 3, having dried out again, showing the phyllaries reopened

Small (1918a) studied hygroscopic movements of the pappus of *C. imperialis* Hausskn. ex Bornm. and found that the pappus is closed fully at 78% humidity but opens fully (to 45°) at 75% humidity. Repeated opening and closing of the phyllaries and pappus with humidity changes possibly also serves to gradually work the achenes loose. Hygroscopic movements of the pappus are readily seen in *C. scabiosa*. In dry conditions the pappus filaments will open to an angle of around 80 degrees to the vertical and close to an angle of around 30° when moistened.

It should be noted that in some species, cleistogamous capitula may occur in which the capitulum does not open at all (presumably neither the phyllaries nor the florets). Cleistogamous capitula may occur in *C. melitensis* as a result of paedomorphosis, specifically progenesis (hypomorphosis) in which development 'switches off prematurely' (Porras & Munoz, 2000).

Finally, it is worth noting that the phyllaries undoubtedly have a protective function. Kaya *et al*. (2010) studied the detailed anatomy of *C. calcitrapa* L. (subsp. *cilicica* (Boiss. & Bal.)) and *C. solstitialis* L. (subsp. *carneola* (Boiss.) Wagenitz) in Turkey and found that the 8-10 collateral vascular bundles in each phyllary incorporated gland canals, the secretion of which perhaps have an anti-fungal or anti-insect function. The frequent presence of spines and fimbriae on phyllaries and their general toughness presumably protect the capitulum from herbivory. Additionally, the upper epidermis possesses stomata and the phyllaries contain photosynthetic chlorenchyma (at least in *C. calcitrapa* and *C. solstitialis*: Kaya *et al*., 2010).

Mechanism of the pappus in wind dispersal

The function of the pappus in dispersal by wind has best been studied in the Dandelion *Taraxacum* agg. The pappus functions as a parachute when the achene is airborne, slowing descent to give wind more time to act and so disperse the seed further. The greater the upwards drag on a falling achene, the slower its terminal velocity. Terminal velocity is the maximum velocity of a falling object and occurs when drag force acting upwards equals the weight of the object acting downwards. The drag force increases with speed of descent so an object falling under gravity eventually reaches a speed at which the drag force is equal but opposite to the weight (weight being the force due to gravity and measured in Newtons).

How effective is a set of filaments compared to a continuous membrane? The mechanics of pappus function in *Taraxacum* agg. have recently been studied by Cummins *et al.* (2018). In their study they combined flow visualisation of achenes in a wind tunnel (using a laser to illuminate air seeded with smoke) and numerical modeling. They found that the filaments of the pappus combine to function like a membrane since the thick boundary layer of relatively still air around each filament helps to negate the spaces between the filaments. The Reynold's number (Re) for flow past a pappus filament is less than 1, meaning that viscous forces dominate (Re can be thought of as the ratio of 'inertial' forces due to bulk fluid flow to resistive viscous forces) such that flow of air past the filament is 'creeping flow'. This means that the pappus, as expected from elementary fluid mechanics, acts somewhat like a continuous membrane in resisting the flow of air.

Cummins *et al.* (2018) also showed that as the air is channeled upwards around the pappus disc of the falling achene, recirculating flow forms a vortex ring above the pappus, which is separated from the main flow. Again, this is to be expected from elementary fluid mechanics, but what Cummins *et al*. (2018) did show, which is really novel, is that the vortex is not shed downstream, which would potentially induce instability in the descent of the achene and furthermore that the flow velocity in the vortex (which rotates counter to the mainstream flow) is only 10% of the mainstream velocity, ensuring that the pressure above the pappus remains low, increasing the drag force acting upwards on the pappus to slow the descent of the achene still further. Crucially the pappus disc does allow some air to creep through the spaces between the filaments, so the pappus functions like a porous funnel, which Cummins *et al*. (2018) observed serves to prevent vortex shedding and so increases both achene stability, and aerodynamic loading on the pappus disc. (The loading, in this context, is the lift generated by the pappus divided by the area of the pappus disc presented to the flowing air, so a higher loading means a more efficient parachute). The porosity of the pappus appears to be finely tuned and presumably depends on the filaments and any barbs they are adorned with. In summary, the pappus evidently has a finely tuned degree of porosity that maximises stability and drag to slow the descent of the achene and thereby decrease terminal velocity.

The pertinent questions to ask now are: why do pappus structures vary so much and how does *Taraxacum* compare to *Centaurea*? Sheldon & Burrows (1973) measured the terminal velocity on achenes from representative species of a number of Asteraceae genera. This included *Taraxacum officinale* Weber. and *Centaurea scabiosa* L. (Greater Knapweed). They obtained a terminal velocity of 35.7 cm/s for *T. officinale* whilst *C. scabiosa* offered the least resistance of the 18 species measured with a terminal velocity of 219.8 cm/s. Interestingly, the 'best' performer was *Tussilago farfara* L. (Colt's-foot) at 19.2 cm/s. They also found that terminal velocity was least in those achenes with the highest pappus diameter relative to achene diameter, though the relationship was not linear.

Actual dispersal distance will also depend on the height from which the achenes are released and after factoring in mean plant height, *C. scabiosa* was predicted to perform a bit better, but still behind *Taraxacum officinale* and *Tussilago farfara*. Predicted maximum dispersal distances in modest winds varied from the order of 1 m in *C. scabiosa* and 1.5 m in *T. officinale* to about 8 m in *Cirsium arvense* (L.) Scop. (Creeping Thistle). How do these predicted values compare to actual measured values?

Mathematical simulations of dispersal in *Taraxacum* agg. suggest that updrafts may disperse a very small proportion of achenes (about one in ten thousand) 1000 m or more, but the vast majority is expected to fall within a few meters (Tackenberg *et al.*, 2003). Some authors have doubted whether so few achenes scattering so far is likely to be important, since the odds of so few seeds finding a suitable habitat appear slim. The situation in *C. scabiosa* seems even worse as far as dispersal over distance is concerned.

Actual measurements are not easy to make, but Roché (1992) used traps to measure achene dispersal in *Centaurea solstitialis* from a planted stand of evenly spaced plants. Roché found that 92% of the achenes were within 0.3 m of the perimeter of the stand and none were trapped more than 9.8 m from the source. Roché concluded that this was compatible with wind dispersal models: *C. solstitialis* has a small pappus relative to the weight and size of its achene and is generally released from a height under 1 m. It can be concluded that although wind dispersal may enable a gradual colonisation of new sites, it seems primarily to serve to scatter seeds over an existing habitat near to and around the parent plant. The importance of dispersal distance is discussed under 'Ecology of achene dispersal' below. *C. solstitialis* was quite a widespread grain, bird-seed, lucerne and wool alien in the British Isles but has declined (Clement & Foster, 1994). It is a native of the Mediterranean.

Small (1918b) studied not only achenes in free-fall but achenes in wind tunnels in order to determine threshold wind speeds needed for dispersal. In *C. imperialis*, it was found that a minimum wind speed of just over 7 mph (11 kph or just over 3 m/s) was needed to make the sedimented achenes airborne inside a glass tube of 4.5 cm diameter.

The genus *Centaurea* exhibits a variety of pappus forms. In *C. cyanus* L. (= *Cyanus segetum* Hill) the pappus is about the same length or slightly shorter that the body of the achene and the filaments are arranged in three rows, the inner and outer rows of shorter scales and the middle row of longer bristles. The filaments are barbed and of the type described as barbellato-setose (barbed setae, Small 1918a) in which the side barbs are of a length comparable to the width of the main shaft. A similar arrangement of three rows of filaments can be seen in the pappus of *C. scabiosa*. What is the significance of this arrangement of pappus filaments?

Walking upwind with the pappus

Whatever the function of the pappus in allowing achenes to be carried downwind on the air, the pappus can also, perhaps surprisingly, assist movement of the achene on the ground. Witztum *et al*. (1996) studied the movement of grounded *Centaurea eriophora* L. achenes in a wind tunnel. *C. eriophora* is an alien known to occur in the British Isles and native to southwestern Europe, northwest Africa and the Canary Islands (Clement & Foster, 1994). The only record on the BSBI database at the time of writing, is from Wharram Quarry (v.c.61, 2018).

Interestingly, Witztum *et al*. (1996) found that whilst on the ground the achenes moved, surprisingly upwind/against the wind at about 10 mm/s in winds of 7 m/s. The achenes oriented with the seed pointing upwind, the pappus downwind. In *C. eriophora* the pappus consists of three rows or circles of hairs: a rigid crown-like inner pappus, an outermost series of short and rigid bristles and between these two a middle row of longer bristles with flexible bases. The mechanism proposed is elastic recoil of the middle row of bristles whose bases are constrained by the stiff inner and outer rows which permitted them to only bend so far. Wind blowing against the achene bends the longer bristles and pushes them against the constraining shorter filaments, storing elastic energy in the pappus. The bristles then recoil elastically, propelling the achene against the wind. The achenes tended to migrate in groups.

Witzum *et al*. (1996) speculated that this ‘walking upwind’ functions in ‘crack seeking’ with the achenes moving upwind until they lodge in suitable crevices, which could give the seeds a clear advantage in germination. It would also mean that dispersal is not restricted entirely to the downwind direction. They found that the achenes of *C. eriophora* were a suitable size for this ‘walking upwind’ at about 4.0 to 4.5 mm in length, 2.3 to 2.4 mm in width and with pappus bristles 6 to 7 mm long. The achenes of *C. scabiosa* have similar measurements. In contrast, *C. hyalolepis* Boiss. (Eastern Star-thistle) has smaller achenes and a smaller pappus and was easily blown away, whilst the achenes of *C. crocodylium* L. were heavier but hairy and so also easily blown away. *C. hyalolepis* is an occasional alien in the British Isles, with the most recent BSBI record, at the time of writing, from The Isle of Wight (v.c.10, 2019).

This arrangement of pappus hairs in three circles, with the inner circle being the longest, is typical in several *Centaurea* species, including *C. scabiosa*. These possibly also make use of this elastic recoil mechanism.

In terms of helping plant achenes orient in soil, it should be noted that seeds may germinate most successfully when oriented optimally (e.g. Bowers & Hayden, 1972). Even a short pappus may cause achenes to land in a certain orientation and perhaps this increases the odds of successful germination. In *Centaurea*, the rootlet emerges near the basal end away from the pappus and opposite to the elaiosome (Viegi *et al*., 2003) so an achene buried pappus-end uppermost will have a better chance of rapid and successful germination. The ovule is orthotropous or erect in *Centaurea* with the radicle emerging below the funiculus (Davis, 1990). Sheldon (1974) observed that achenes of *Taraxacum* agg. germinate most successfully, on a flat surface, when the long axis is at 45° to the horizontal with the hilum in contact with the surface to imbibe water. This is the natural position of the achene when it lands with an intact pappus.

It has been suggested that the pappus of *Centaurea* may serve a similar function in orienting the achene (Davis, 1990). Studying *C. maculosa* L. (Spotted Knapweed) Davis observed that the pappus opens to 45 to 60 degrees then remains permanently in this position, regardless of further changes in humidity. This could serve to orient the achene in an optimum position to imbibe water which was observed to occur through the hilum and the disc-nectary tissue around the micropyle. The hilum is lateral, adaxial and towards the basal end of *Centaurea* achenes. In contrast the pappus of *C. scabiosa* opens and closes repeatedly with changes in humidity.

The importance of the elaiosome

The achenes of many *Centaurea* species are equipped with an elaiosome, an appendage of tissue rich in lipids and/or protein and/or starch (see Table 1). Many authors seem to have overlooked these structures when studying achene morphology, perhaps because they occur around the hilum and so may have been mistaken for ordinary scar tissue. Generally, studies on the function of these elaiosomes are lacking. Witzum *et al*. (1996) placed achenes of *C. eriophora* in areas where harvester ants (*Messor* sp.) foraged and found that the ants grasped the achenes by their elaiosomes and carried them off.

The elaiosome of *C. maculosa* consists of a honeycomb of maternal receptacle tissue (Davis, 1990). Although the hilum imbibes water for germination, and has waxy pores on its surface which may assist in this (Davis, 1990), removal of the elaiosome has a small effect on the percentage of germination in controlled experiments, either increasing it or decreasing it slightly, and may shift the time of germination up to a few days in either direction depending on species (Viegi *et al*., 2003). Any direct role of the elaiosome in germination therefore remains unclear.

It should also be noted that the elaiosomes are often accompanied by a surrounding series of bristles. These can be clearly seen in *C. scabiosa*, for example, and their function is unknown.

Heteromorphic achenes

Centaurea solstitialis has two achene types in the same capitulum and their dispersal has been studied by Joley *et al*. (1997) and Roché (1992). In the centre of the capitulum are produced light-coloured achenes with a pappus consisting of two rows of bristles and in California, these are dispersed first in the summer. The remaining achenes are dark-coloured and remain in the capitulum until winter when the involucral bracts loosen to release them or until the phyllaries fall off after repeated wetting and drying during the autumn and winter (Roché 1992). The outermost circle of florets is sterile.

As achenes mature the receptacle of *C. solstitialis* dries and contracts, forcing the detached achenes upwards. As the pappus dries it opens, causing the achenes to separate and disperse, whilst moisture closes the phyllaries, retaining the achenes (Roché 1992). The receptacle scales in the *C. nigra* group perhaps function in a similar way by pushing the achenes out as the capitulum dries.

Heteromorphic achenes also occur in *C. melitensis* (Bain, 2015). Within the same capitulum the peripheral achenes are lighter and narrower with shorter pappi and reduced elaiosomes. However, no differences in germination or length of time the two achene types remain in the capitulum could be found (Bain, 2015). Additionally, this species produces both chasmogamous and cleistogamous capitula. The smaller cleistogamous capitula have larger achenes with a smaller pappus length to achene diameter ratio (Bain, 2015).

Other dispersal mechanisms

Centaurea diffusa Lam. (Diffuse Knapweed, White Knapweed or Tumble Knapweed) is a native of the eastern Mediterranean and an occasional alien visitor to Britain. The capitula of this species detach by abscission to be blown along by the wind: they tumble. This mechanism has been studied by Baker *et al*. (2010). Tumbling can be especially effective for long-distance dispersal (LDD, defined as distances exceeding 100 m from the parent plant) as long as the achenes are not all shed too quickly. A small opening in the capitulum of *C. diffusa* enables achenes to be gradually released. Although most are released early on, a significant number can be transported for distances exceeding one kilometer (Baker *et al*., 2010).

Roché (1992) considered the possible role of birds as dispersal agents of *C. solstitialis*. Roché considered finches possible agents in occasional LDD events, but only if they accidentally dropped the achenes or swallowed them whole since they normally shell seeds before eating them. Roché notes, however, that achenes may potentially pass through the guts of pheasants and remain viable, as reported by Thill *et al*. (1986) for Chinese Pheasants (*Phasianus colchicus*) eating achenes of *Cuprina vulgaris* (False Saw-wort).

Von der lippe & Kowarik (2007) carried out extensive sampling of seeds/fruit of native and non-native flora deposited in road tunnels in Berlin and found that vehicles transport and deposit 635 to 1579 seeds/m^2/year, which is a considerable quantity. Non-native species were particularly well represented in their samples, suggesting that roads represent a major route for LDD.

Pearson & Ortega (2001) studied *C. maculosa* dispersal and concluded that vehicles, humans and livestock were all important, whilst Deer Mice (*Peromyscus maniculatus*) searching for gall fly larvae (*Urophora* spp. which overwinter in the capitula and act as biocontrol agents) accidentally ingest whole seeds; whilst 1% of achenes retrieved from Great Horned Owl (*Bubo virginianus*) pellets germinated.

Ecology of achene dispersal – near and far

In the western USA *Centaurea* has been described as the most 'noxious weed' and is also highly invasive in Canada. LeJeune & Seastedt (2001) referred to *Centaurea* as 'the forb that won the West'. In particular, five species have been especially invasive in North America: *C. solstitialis*, *C. diffusa*, *C. maculosa*, *C. virgata* Lam. and *C. repens* L. (LeJeune & Seastedt, 2001).

There have been attempts to explain invasiveness in terms of resource acquisition and sequestration, particular nitrogen, phosphorous and water (LeJeune & Seastedt, 2001) and these are no doubt important. However, others have stressed the potential importance of dispersal mechanism, in particular mechanisms favouring LDD events though these studies tend to be theoretical and based on modeling due to the difficulties in collecting actual data on LDD (e.g. Kot *et al*. 1996, Clark *et al*. 1999). However, genetic studies offer a practical solution to this problem (Cain *et al*. 2000) though genetic analysis is a measure of dispersal and establishment rather than dispersal *per se*. The conclusions of such studies are: i) that the tail of the probability distribution (distribution kernel) i.e. those few achenes that disperse far, warrants more emphasis and ii) more data need to be collected. In other words, although infrequent, LDD events appear to be ecologically important.

Even if wind does not readily lend itself to LDD in *Centaurea*, I have already discussed the importance of vehicles (Von der lippe & Kowarik, 2007) animals and birds (Roché, 1992, Pearson & Ortega, 2001) and tumbling in *C. diffusa* (Baker *et al*., 2010). The impact of these agents of dispersal on species invasiveness and also on connecting fragmented habitats warrants further study.

Short-distance dispersal is also of ecological significance. In particular, mathematical models suggest that short-distance dispersal may help tetraploids forming sporadically as a minority in a diploid population to better establish and spread. Baack (2005) argues that any tetraploids that arise may be at a distinct competitive disadvantage when surrounded by pollinating diploids due to the formation of sterile triploid zygotes through mixed-ploidy crosses. In his computational model short-range dispersal increases the likelihood of a tetraploid being pollinated by other tetraploids, by establishing a local population and increased their survival and eventual global spread, even without autogamy.

Interestingly, reproductive isolation between populations of different ploidy in *Centaurea* have been found to be due to post-zygotic barriers, that is the pollen is accepted and fertilisation occurs, but results in failed zygote development (Koutecký *et al*., 2011). Therefore, Baack's mechanism could well operate in *Centaurea*. Furthermore, the occurrence of tetraploids is characteristic of the *C. nigra* group. *C. nigra* and *C. jacea* occur as both diploid (2n=22) and tetraploid (2n=44) forms (see: eFlora of North America and Stace, 2019). *C. debeauxii* is generally recorded as a tetraploid (2n=44, Stace 2019) but diploid forms have been reported in North America (www.cabi.org/isc/datasheet/113056). Could it be that the reduction in the pappus seen in this group was selected for, as it favoured the spread of the tetraploid populations by increasing short-distance dispersal?

Conclusion: Further Questions Raised

There is much still to be learnt about the fascinating story of achene dispersal in *Centaurea* and its roles in ecology and evolution. Is reduction of the pappus linked to tetraploidy? Why do some species have a reduced pappus rather than no pappus at all? What modes of long-distance dispersal are operating in the British Isles? What is the function of achene hairs? Do hygroscopic movements occur in the pappus and phyllaries of other species? Careful observations can fill in the gaps in our knowledge for other *Centaurea* species which may shed more light on the bigger picture relating to ecology and ploidy. Finally, an important application is to further investigate the importance of dispersal mechanism, over both short and long distances, in the invasiveness of *Centaurea* species. It is hoped that this review will prompt further interest in these fascinating topics.

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