



Clonal splitting in desert shrubs

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Abstract

Axis splitting is a widespread phenomenon in desert shrubs, and has been reported for shrubs from several plant families, both in old- and new-world deserts. It is so common in dwarf shrubs of arid environments as to be a defining characteristic of this growth form. Although anatomists described this phenomenon several decades ago, there has been only one ecological study of one species, *Ambrosia dumosa*. The anatomical nature of the various splitting mechanisms that have been found suggests axis splitting to be an extreme form of hydraulic segmentation. The adaptive advantage of clonal splitting in desert shrubs has yet to be determined, but it appears to be largely a risk-spreading mechanism that enables independent mortality of integrated hydraulic units (IHUs) or ramets. This should be especially advantageous in heterogeneous, water-limited environments, where soil water occurs in pockets too small to support a large shrub-genet. Clonal splitting may cause an increase in intracolonial competition among ramets, but there are also indications that at least some species possess mechanisms to reduce competition by minimizing root system overlap among ramets. Many desert shrub species that undergo clonal splitting maintain a dense clump growth form, possibly because such a growth form has positive effects on water and nutrient status of the soil and long-term effects on other soil properties.

Introduction

Desert shrubs, such as *Ambrosia dumosa*, *Acamp-topappus sphaerocephalus* and *Coleogyne ramosissima* in the Mojave Desert of North America or *Artemisia herba-alba* and *Peganum harmala* (for authorities see Table 1) in the deserts of southwestern Asia are rarely thought of as clonal plants; they do not grow by means of stolons or rhizomes and produce no root suckers. Yet, they invariably split along their axes into clonal fragments once they attain a certain size (Figures 1 and 2). To the casual observer split plants are often indistinguishable from unsplit ones. Plant ecologists also have paid scant attention to this type of clonality. Recent edited volumes on the biology of clonal organisms (de Kroon & van Groenendael 1997; Jackson et al. 1985; van Groenendael & de Kroon 1990) do not mention it. It is also not included in the classification systems of clonal growth in plants pro-

posed by Tiffney & Niklas (1985) and specifically for woody plants by Peterson & Jones (1997).

Axis splitting has been found in a number of families, including the Aizoaceae, Asteraceae, Boraginaceae, Fabaceae, Frankeniaceae, Fumariaceae, Geraniaceae, Lamiaceae, Onagraceae, Ranunculaceae, Rosaceae, Solanaceae, and Zygophyllaceae (Bowns & West 1976; Fahn 1964; Ginzburg 1963; Jones & Lord 1982; Kutschera & Lichtenegger 1992; Mikhailovskaya 1967; Moss & Gorham 1953; Vasilevskaya & Shokina 1968; Wallace & Romney 1972; Werger 1986; Whalen 1987) (Table 1). It is particularly common in shrubs from arid and semi-arid environments (Fahn 1964; Vasilevskaya & Shokina 1968). Many of the dominant shrub species that cover vast areas of the North American, Asian, and North African deserts are clonal splitters, for example *Larrea tridentata* and *Ambrosia dumosa* in the Mojave Desert (MacMahon & Wagner 1985), and *Zygophyllum dumosum* and *Artemisia herba-alba* in the Negev Desert

Table 1. Shrub species from arid and semi-arid environments that have been found to regularly undergo clonal fragmentation by means of axis splitting.

Plant family	Old world	New world
Zygophyllaceae	<i>Zygophyllum dumosum</i> Boiss. ¹ <i>Peganum harmala</i> L. ¹	<i>Larrea tridentata</i> (DC.) Cov. ^{2,3,11}
Asteraceae	<i>Rhanterium suaveolens</i> Desf. ⁸ <i>Eriocephalus pubescens</i> DC. ¹² <i>Artemisia herba-alba</i> Asso ^{1,*} <i>Artemisia ordosica</i> Krasch. ⁹ <i>Artemisia campestris</i> L. ssp. <i>glutinosa</i> (J. Gay) Batt. ⁸ and many other species of <i>Artemisia</i> ⁵	<i>Acamptopappus sphaerocephalus</i> (A. Gray) A. Gray ^{10,11} <i>Ambrosia dumosa</i> (A. Gray) Payne ^{4,11} <i>Artemisia spinescens</i> D. Eaton ¹¹ <i>Hymenoclea salsola</i> A. Gray ¹¹ <i>Ericameria cooperi</i> (A. Gray) H. M. Hall ¹¹
Brassicaceae	<i>Zilla spinosa</i> (L.) Prantl ¹	
Fabaceae	<i>Astragalus</i> spp. ⁵	
Frankeniaceae		<i>Frankenia jamesii</i> Torrey ⁷ <i>Frankenia johnstonii</i> Correll ⁷
Aizoaceae	<i>Plinthus karoocicus</i> Verdoorn ¹²	
Chenopodiaceae	<i>Salsola gemmascens</i> Pall. ⁵ <i>Salsola vermiculata</i> L. ⁸	
Rosaceae		<i>Coleogyne ramosissima</i> Torrey ^{3,6,11}
Solanaceae		<i>Lycium andersonii</i> A. Gray ^{3,11}

¹Ginzburg (1963); ²Vasek (1980); ³Wallace & Romney (1972); ⁴Jones & Lord (1982); ⁵Nechaeva (1985); ⁶Bowns & West (1976); ⁷Whalen (1987); ⁸Bendali et al. (1990); ⁹Kobayashi et al. (1995); ¹⁰Gibson (1996); ¹¹Personal observation; ¹²Werger (1986). Nomenclature follows that of the references cited, except for plants indicated by superscripts 2, 3, 4, 6, and 11, where the nomenclature follows Hickman (1993).

*Plants formerly referred to as *Artemisia herba-alba* Asso from Israel are included today in *A. sieberi* Besser by some authors, while plants from Tunisia have been included in *A. inculta* Del. All three of these taxa have been placed in the genus *Seriphidium* (Besser ex Hook.) Fourr. by some authors, and all three are clonal splitters (Ginzburg 1963; Ourcival et al. 1994; C. Holzzapfel, University of California Santa Barbara, personal communication).

of Israel (Evenari et al. 1982). Clonal splitting is so common in dwarf shrubs of central Asia, e.g., in the genus *Artemisia*, as to be a defining characteristic of this group of woody plants (Nechaeva 1985; Nechaeva et al. 1973). Clonal fragmentation has received more attention in the Russian than in the English literature, and in translations from the Russian it is often referred to as particulation (Barykina 1995; Gatsuk et al. 1980; Vasilevskaya & Shokina 1968).

The purpose of this paper is to review mechanisms and patterns of clonal splitting in desert shrubs and put it into the context of current clonal plant research. Potential causes and ecological consequences of this phenomenon are discussed. Some approaches are outlined and illustrated by original research that may help to answer the question why clonal splitting is so common in desert shrubs.

Morphology of clonal splitting in desert shrubs

For a discussion of detailed anatomical and morphological characteristics of axis splitting the reader is referred to the literature cited. Briefly, splitting of roots, rhizomes, and stems may occur as a result of interxylary cork formation, including suberization of xylem rays, or simply as a result of differential cambial activity, which leads to the formation of grooves and lobes in the wood (Fahn 1982; Fahn & Cutler 1992; Ginzburg 1963; Jones & Lord 1982; Moss & Gorham 1953; Whalen 1987). This creates a fluted to segmented axis (Figures 3b and 3c). In some desert shrub species that possess deeply-fluted axes, splitting is only rarely observed; instead, the heartwood in the center of the axis remains to give mechanical support to the stem. Examples for this are large shrubs such as *Artemisia tridentata* Nutt. (Ferguson 1964) and *Atriplex confertifolia* (Torrey & Frémont) S. Watson (Figure 3b). In other cases, the axes almost

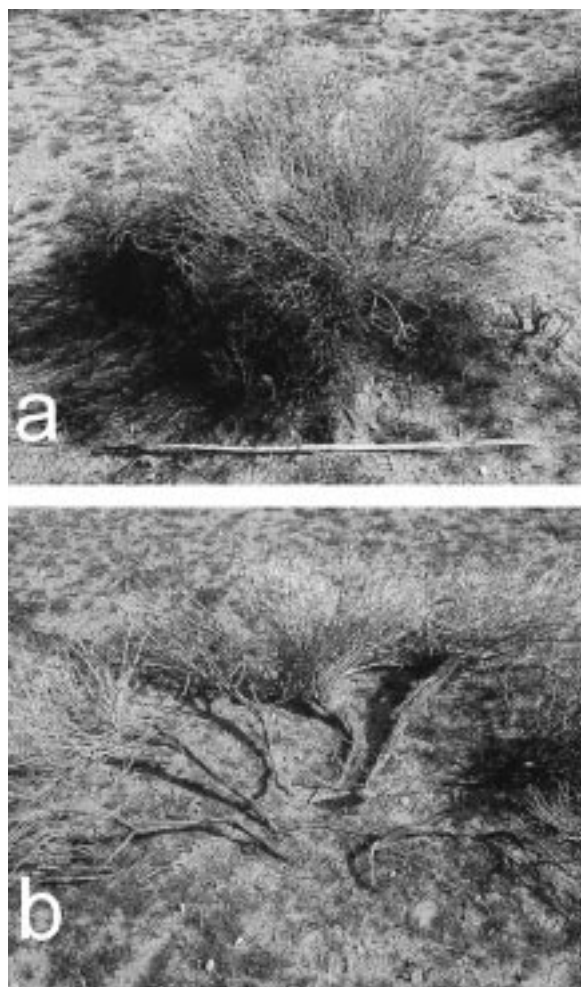


Figure 1. The small desert shrub *Acamptopappus sphaerocephalus* (Asteraceae), common in the Mojave Desert of North America. (a) A large, vigorous shrub genet of about 1 m diameter. (b) The same genet after excavation proves to be split into separate ramets.

invariably mechanically break up along the grooves between the segments and the heartwood rots away. Examples for this are many dwarf-shrubs, such as *Ambrosia dumosa*, *Ericameria cooperi*, and *Acamptopappus sphaerocephalus* (Figure 3c). In these species, major branches of the old tap root functionally become tap roots for the clonal fragments (= ramets). Large specimens of such species nearly always consist of separate ramets (Figure 2), but even small specimens may have a highly divided axis (Figure 3c). It has been suggested that splitting may be a sign of senescence (e.g., Nechaeva 1985), but at least in the new world species listed in Table 1, the degree of fragmentation is most pronounced in large and vigorous shrubs (e.g., Figure 2). While fluted and segmented axes are ex-

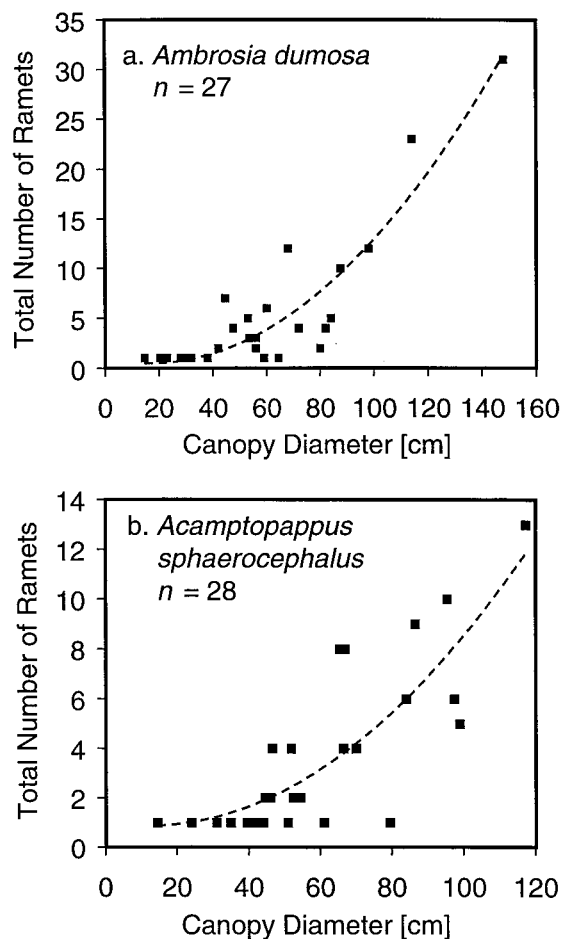


Figure 2. Number of physically separate ramets, including live and dead ones, in shrub genets of two species from the Mojave Desert, North America, as a function of the canopy diameter of the genet. (a) *Ambrosia dumosa*. (b) *Acamptopappus sphaerocephalus*. In both cases, shrubs larger than 50 cm diameter are usually split into two or more ramets. At the same size, *Ambrosia* has on average more separate ramets than *Acamptopappus*. All of the shrubs sampled were vigorous specimens that showed no visible senescence of the canopy.

ceedingly common in desert shrubs, there are also a number of species, e.g., *Encelia* spp. (Figure 3a), that have the same round axes as most shrub species from mesic habitats.

Fragmentation of the genet physically splits it into a number of functional individuals (*sensu* Vuorisalo & Tuomi 1986) or ramets. In the following, the term ramet will be used for these functional units, because ramets are generally understood to be units consisting of a shoot- and a root-system, and the term does not imply physical independence. It should be understood, however, that ramets in axis splitters are different from

those in many other clonal plants in that they are not morphologically distinct before the actual split. After a complete lengthwise split along the main stem- and root-axis, former branches and lateral roots become the main axes of the ramet, in time often becoming virtually indistinguishable from axes of younger, unsplit individuals. All splitting desert shrub species examined in this review (see Table 1) had fairly shallow, generalized root systems (Cannon 1911), with the majority of roots in the upper 1 m of the soil profile and with major lateral roots spreading at an angle or horizontally at between 0.1 and 0.5 m depth. When these laterals become separated from the old tap root, no connections to other lateral roots remain at greater depth, contrary to a suggestion by Ebert & McMaster (1981) regarding *Larrea tridentata*.

It is important to note that, even without a physical split, ramets can function as completely independent, integrated physiological units (Watson & Casper 1984). Thus, splitting may be either the cause for ramet independence or a consequence of a high degree of branch autonomy (Sprugel et al. 1991). Whether a species physically splits once it reaches a certain stage in its ontogeny probably depends on a variety of factors, including wood anatomy, root system morphology, shrub height, and, of course, phylogenetic constraints. In small shrubs, maintenance of physical connections between physiologically independent modules may simply be unnecessary or even costly. In taller shrubs, intact, main axes are needed for mechanical support, but branches may still be completely autonomous and may receive water and nutrients from separate parts of the root system (Waisel et al. 1972). The following discussion of the ecological functions of clonal splitting in desert shrubs also pertains to species that are functionally, but not physically, split.

Ecological function of clonal splitting in desert shrubs

Previous hypotheses

Axis splitting in desert shrubs has been widely described and studied from morphological and anatomical perspectives, but few authors have discussed the question why this is so common in desert shrubs. To my knowledge, only one author, C. S. Jones (1984), has ever attempted to test some of the hypotheses voiced by earlier authors to explain this phenomenon. The possibility that the prevalence of axis splitting



Figure 3. View of cross-sections of the main stem axes of three North American desert shrubs, cut near ground level and viewed from below. (a) *Encelia farinosa* Torrey & A. Gray (Asteraceae), round cross-section. (b) *Atriplex confertifolia* (Chenopodiaceae), deeply-fluted axis with intact heartwood. (c) *Ambrosia dumosa* (Asteraceae), fluted and split axis, heartwood does not persist.

in desert shrubs may be partly a phylogenetic effect currently cannot be ruled out. Axis splitting appears to have evolved many times independently (Moss & Gorham 1953), but it may be restricted to certain families and genera and/or certain environments. It is certainly a taxonomically widespread phenomenon (see Table 1). The remainder of this discussion will

focus on the potential adaptive significance of axis splitting in desert shrubs, without thereby implying the absence of phylogenetic effects.

In many descriptive studies of clonal fragmentation, this phenomenon was interpreted simply as age-related, and the authors did not attribute any selective advantage or disadvantage to it (e.g., Gatsuk et al. 1980; Nechaeva 1985). However, the hypothesis that clonal fragmentation is selectively neutral does not explain why it appears to be more common in woody plants from arid and semi-arid environments than in those from mesic environments. Ginzburg (1963) was one of the first authors to address this question when he suggested that axis splitting may be one of many abscission phenomena often observed in desert shrubs (Orshan 1972; Orshan & Zand 1962). According to Ginzburg, axis splitting may enable that part of the plant in the most favorable microhabitat to survive and reproduce, while other parts are abscised to reduce the transpiring area. This assumes that competition for water among plant parts is an important aspect of the fitness of desert plants. However, this explanation does not appear to be valid for the many drought-deciduous species that show clonal splitting. To quote Fahn (1964 p. 95): "As no foliage actually remains on desert plants during the dry season, the main problem of adaptation is not by which means transpiration is reduced in the leaves but how the plant remains viable until the next rainy season. The answer must therefore be sought in the axis of the plant."

On the other hand, the assumption that those ramets in the most 'favorable microhabitat' have a higher chance of survival than others in less favorable ones (Evenari et al. 1982; Gibson 1996; Ginzburg 1963; Orshan 1972) appears to be sound. Most favorable here only means a microhabitat that enables survival during a critical drought period, not necessarily one that consistently offers better conditions throughout the growing season as suggested by Jones (1984).

Clonal splitting of desert shrubs as a risk-spreading mechanism

A number of theories have been set forth to explain functions of clonality, and these may be divided into two categories: resource acquisition and risk spreading (Cook 1983; de Kroon & van Groenendael 1990). It is difficult to see how clonal fragmentation in itself could facilitate resource acquisition. Spreading of the canopy and root system may reduce intraclonal competition for light and soil resources and improve the

efficiency of foraging for resources but these effects are not dependent on clonal fragmentation. Axis splitting in desert shrubs may facilitate some spreading of the canopy and allow the formation of large clonal patches or rings in some species, for example in *Larrea tridentata*, species of *Lycium*, and in *Artemisia monosperma* (Danin & Orshan 1995). But in many other species, ramets of split plants remain tightly aggregated and little spreading of the canopy is evident (e.g., Figure 1).

This brings us to risk spreading, the other proposed function of clonality. If the fates of ramets are more or less independent, then adding new ramets can increase the potential longevity of the genet (Cook 1983; Eriksson & Jerling 1990; Watkinson & White 1985). This may be described as a clonal survival strategy as opposed to a clonal growth strategy, and Peterson & Jones (1997) have suggested that this type of clonality is more common in woody plants than clonal foraging.

The idea that clonal splitting of desert shrubs increases the chance of genet survival is not a new one, but previous authors have always postulated that partial death of the genet should increase the chances of survival for the remaining parts of the genet (Evenari et al. 1982; Ginzburg 1963; Orshan 1972). This implies that module mortality is not independent. An alternative hypothesis is that mortality of modules may be independent (Cook 1983; Eriksson & Jerling 1990; Watkinson & White 1985). In this case, assuming an equal chance of mortality for each module, the probability of genet extinction (P_{genet}) during any time period (e.g., a drought) is $P_{\text{genet}} = P_{\text{module}}^n$, where P_{module} is the probability of module death during the period, and n is the number of modules. Thus, increasing the number of independent modules decreases the probability of genet death. Available data on mortality rates of desert shrubs during periods of drought suggest that a single drought year rarely kills more than 20% of the individuals in a population, but that prolonged periods of drought can cause much higher mortality (Watson et al. 1997). Assuming a chance of module death of 50% during a long drought, a genet consisting of one, physiologically integrated module will have a probability of extinction of $P_{\text{genet}} = 0.5$. In contrast, a genet consisting of 10 independent modules, each with a probability of death of $P_{\text{module}} = 0.5$, would have a probability of extinction of 0.000977. This probability would be even lower if death of modules increased the survival chances of the remaining modules (Evenari et al. 1982; Ginzburg 1963; Orshan

1972), but it would be higher if the death of modules increased the vulnerability of remaining modules.

Based on these calculations, one would expect clonal splitters to be long-lived and this appears to be the case. The longevity of *Larrea tridentata*, estimated up to 11 700 years (Vasek 1980), is almost legendary, and a recent study using repeat photography found that the clonal shrubs *Lycium andersonii* and *Ambrosia dumosa* can live longer than 100 years (Bowers et al. 1995). In contrast, the aclonal *Encelia farinosa* (Figure 3a) appears to rarely reach ages of greater than 50 years (Bowers et al. 1995; Goldberg & Turner 1986; Szarek et al. 1997).

Axis splitting in desert shrubs as a form of hydraulic segmentation

Clearly, the advantages of risk spreading should apply to all plants in all habitats, but the evidence suggests that clonal splitting is far more common in plants from arid and semi-arid environments than from mesic environments (Vasilevskaya & Shokina 1968). This is because there are also disadvantages to module independence, or to put it the other way, advantages to physiological integration (Jónsdóttir & Watson 1997; Vuorisalo & Hutchings 1996; Watson & Casper 1984). Physiological integration is usually discussed in terms of carbon allocation (Caraco & Kelly 1991; Jónsdóttir & Watson 1997; Watson & Casper 1984) or nutritional integration (Jónsdóttir & Watson 1997; Marshall 1990; Pitelka & Ashmun 1985; Price et al. 1996), both of which are largely due to the activity and vascular architecture of the phloem. Mineral nutrients are transported from the roots to aboveground organs mainly in the xylem's transpiration stream, but remobilization of nutrients and subsequent transport between plant organs largely takes place in the phloem (Marschner 1995). In contrast, hydraulic integration is almost exclusively a function of the vascular architecture of the xylem (Sprugel et al. 1991; Tyree & Ewers 1991). Incomplete physiological integration with regard to carbon, minerals, and hormonal signals has been termed sectoriality (Vuorisalo & Hutchings 1996; Watson & Casper 1984). This should not be confused with the sectoriality of water flow often found in the xylem of woody plants from arid habitats (Waisel et al. 1972). It is probably better to use the term hydraulic segmentation (Zimmermann 1983) for the sectoriality of water flow to set it apart from physiological sectoriality. Segmentation and sectoriality may frequently co-occur, but they are not identical.

Axis splitting affects both physiological and hydraulic integration, but there are good reasons to view it mainly as an extreme form of hydraulic segmentation. Firstly, in all known cases, axis splitting is a function of xylem structure and thus a consequence of certain patterns of secondary growth (Fahn 1982; Fahn & Cutler 1992; Ginzburg 1963; Jones & Lord 1982; Whalen 1987). Secondly, axis splitting has most often been reported from woody plants of water-limited environments, which also have other mechanisms of hydraulic segmentation, e.g., sectorial patterns of water ascent in the xylem (Waisel et al. 1972), interxylary cork and/or suberized wood rays (Fahn 1982; Ginzburg 1963). Thirdly, the fact that axis splitting appears to be most common in plants from dry habitats suggests that water limitation is an important factor.

Because a split axis breaks all vascular connections, transport of carbon, nutrients, and hormonal signals, as well as that of toxins and pathogens is also inhibited. Blockage of toxin- and pathogen-spread is certainly an advantage of clonal fragmentation (Shigo 1985; Silander 1985; Sprugel et al. 1991), but a lack of integration with regard to water, carbon, and nutrients may have serious disadvantages for plants. Physiological and hydraulic integration enables plants to share resources between modules of different resource-status, which is especially advantageous in environments where the placement and structure of modules causes or allows some degree of module specialization (Alpert & Stuefer 1997). For example, some modules may be placed in high-light, water-limited environments, while others are in low-light, mesic environments. In general, it has been found that a high degree of physiological integration is common in clonal plants that grow in resource-poor, heterogeneous environments (Jónsdóttir & Watson 1997). A potential disadvantage of integration is the possibility of 'selfish', competitive interactions among modules (Hardwick 1986; Vuorisalo & Hutchings 1996). It has been found that sectoriality with regard to carbon, nutrients, toxins, and hormonal signals is often under some degree of developmental and physiological control (Marshall & Price 1997; Vuorisalo & Hutchings 1996; Watson & Casper 1984), which allows plants to maximize the benefits and limit the negative effects of physiological integration.

In contrast, plants have much less control over the gradients of water potential that govern water transport. Water always flows in the direction of the more negative water potential, and the only way to decouple water flow is by blocking the xylem, for example by

cavitation or by structural modifications, such as junction constrictions of the xylem (Tyree & Ewers 1991; Zimmermann 1983) or interxylary cork layers (Fahn 1982). The main mechanism to regulate xylem pressure potential gradients is stomatal regulation (Nobel 1991), although other mechanisms, such as osmotic ones, may also play a role (Grace 1993; Salleo et al. 1996; Zimmermann et al. 1994). In woody plants from arid environments, physiological controls over water potential gradients do not appear to be sufficient to prevent water-stressed modules from negatively affecting other modules, because there is abundant evidence that such plants often possess a high degree of structural, hydraulic segmentation (Fahn 1964; Fahn & Cutler 1992; Waisel et al. 1972).

Module mortality induced by drought stress is caused by xylem cavitation (Grace 1993). This creates the potential problem of 'runaway embolism', a loss in hydraulic conductivity which would itself cause more cavitation, and could affect large parts of a plant (Tyree & Ewers 1991). Hydraulic segmentation provides a safeguard against this situation by restricting cavitations to particular branches and leaves (Grace 1993; Tyree & Ewers 1991; Zimmermann 1983). Hydraulic independence of modules in desert shrubs may well have the same function on a whole plant level. Clonal splitting prevents water-stressed plant modules from negatively affecting other modules, thereby decoupling module mortality (Sprugel et al. 1991). Whether this is the main adaptive advantage of clonal splitting in desert shrubs or one of several remains to be investigated. In this context it would be instructive to explore the question whether clonal splitters differ from acclonal desert shrubs in their vulnerability to embolism (S. Schwinning, University of Utah, personal communication).

Clonal splitting in a heterogeneous environment

Previous research on clonal plants has shown that the degree and characteristics of environmental heterogeneity often have a large influence on clonal plant behaviour (Stuefer 1996). In the above discussion, a heterogeneous distribution of the resource water has been assumed to sometimes exist within plants. Where this is rarely or never the case, hydraulic segmentation would have no advantages, as all modules would share a similar water status. Where notable differences in water status among modules do occur, they are likely to be largely a result of environmental heterogeneity.

Under what conditions does module independence with regard to water status appear to be a favorable strategy? Where soil moisture is distributed rather homogeneously in the soil volume, hydraulic independence of modules would appear to be a neutral or even disadvantageous trait, because integrated genets could balance slight differences in water potential among modules. If soil moisture is distributed heterogeneously but is not limiting plant performance, hydraulic integration would enable sharing of water among modules, regardless of their spatial placement. Only where water is limiting and heterogeneously distributed in small pockets, may individual modules have a higher chance of survival by not sharing water with other modules, especially if the pockets are typically too small to support the whole genet.

The density, distribution, and size of patchy resources should at least partly determine whether integration or disintegration is the better survival strategy for the genet. For example, desert shrubs that grow in very rocky habitat may be able to access rather large resource pockets in rock clefts with only one major root, which could potentially support the whole genet. In such plants, hydraulic integration could be a successful strategy. Phreatophytic shrubs that access deep water resources with a single taproot can also be expected to be hydraulically tightly integrated. In contrast, many shrubs that grow on the gravelly to rocky substrates of piedmont slopes are relatively shallowly-rooted (Cannon 1911; Cody 1986; Evenari 1938). They mostly rely on soil moisture resources from precipitation and runoff stored in the upper metre of the soil profile (Schlesinger & Jones 1984). For such plants, small pockets of moisture under stones are often the only remaining soil resources during a dry season (Evenari et al. 1982). Hydraulic integration of the genet would only be beneficial for shrubs in such habitats if they could access enough pockets of soil moisture to support the whole genet. A small pocket of soil moisture may not be enough to support a whole shrub but it may enable the survival of a small ramet if the water is not shared with other ramets. Based on these considerations, one would expect that shallowly-rooted shrubs are more likely to be clonal splitters than deep-rooted ones and this is indeed the case. Woody desert phreatophytes of the North American deserts, such as *Prosopis glandulosa*, *Acacia gregii*, *Olneya tesota*, and *Chilopsis linearis*, show no signs of axis splitting, while shrubs typical of piedmont slopes, such as *Larrea tridentata*, *Ambrosia*

dumosa, *Ericameria cooperi*, and *Acamptopappus sphaerocephalus* are clonal splitters (Table 1).

Competition among ramets

Many plants are organized into largely autonomous integrated physiological units, or IPUs (Hutchings & Mogie 1990; Watson & Casper 1984). Hydraulically segmented plants are split into what may be called integrated hydraulic units, or IHUs, which may or may not be identical with IPUs. Within these IHUs, the flow of water follows gradients of water potential towards sinks, usually leaves (Nobel 1991). While the stomata are open, leaves differ in their sink strength, depending on their placement in the canopy and their physiological status, thus modules within the IHU generally compete for water. During the night, the water potential within the whole IHU reaches an equilibrium, the so-called predawn water potential, and competition ceases. In contrast, separate IHUs potentially can compete for water at all times and their predawn water potentials can differ significantly, as has been shown for *Ambrosia dumosa* (Jones 1984).

Competition among IHUs can potentially have a negative impact on inclusive genet fitness, for example when energy is expended to place roots of separate IHUs into close proximity. This type of competition may be termed scramble competition, defined as the use of a common resource when the supply is inadequate for all and is limiting to the competitors (McIntosh 1992). The costs for scramble competition can potentially be lowered when the roots of IHUs are placed in separate parts of the soil volume, either because of a constrained rooting morphology or because of direct negative interactions among roots of IHUs (Schenk et al. in press), as reported for the desert shrubs *Ambrosia dumosa* and *Larrea tridentata* (Mahall & Callaway 1992, 1996). These two species have been found to possess very different mechanisms to minimize root-overlap, but in both cases, the mechanisms operate among separate ramets, and, in the case of *Larrea tridentata*, also within ramets. This type of competition may be termed contest competition, because a chemical inhibition limits access to a common resource (McIntosh 1992). Costs of scramble and contest competition are often difficult to compare, but it has been found that scramble competition is often more costly (Wilson 1975), and thus would tend to have a greater negative impact on the inclusive fitness of the genet. It is suggestive that both of these species are clonal splitters and that both pos-

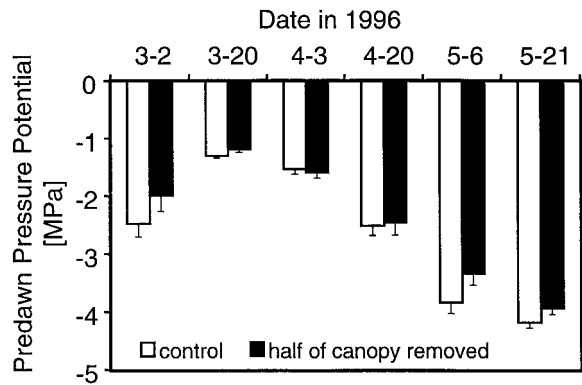


Figure 4. Effects of partial ramet removal on the water status of large (>90 cm diameter) shrub genets of *Ambrosia dumosa* in Fremont Valley, Mojave Desert, California. For removal treatments ($n = 10$), half of the canopy was removed by cutting the branches at ground level on March 1, 1996, while control shrubs ($n = 10$) were left intact. Predawn pressure potentials were measured approximately every two weeks from March 2 to May 21, 1996, using a pressure bomb (Scholander et al. 1965). Shown are the means of 10 replicates \pm one standard error. For statistical analysis, the results were multiplied by -1 and log-transformed to normalize the distributions and analyzed in a repeated measures ANOVA using the MGLH-routine in SYSTAT (Wilkinson 1990), with treatment as grouping factor. The overall treatment effect was significant at $p = 0.047$ ($df = 1$, $SS = 0.055$, $F = 4.56$; error: $df = 18$, $SS = 0.218$). In summer 1996, the shrubs used in the removal treatments were excavated to determine whether the removed part of the canopy had been physically separated from the remaining parts; this was true in all cases.

sess mechanisms that can potentially reduce scramble competition within genets.

One way to test for competition among IHUs for resources external to the plant is by partial removal of IHUs within genets. Such a study, conducted in the northwestern Mojave Desert of North America, revealed that removal of IHUs had a positive effect on predawn water potentials of the remaining IHUs of the desert shrubs *Ambrosia dumosa* (Figure 4). A similar trend was found for *Acamptopappus sphaerocephalus* in the same location (data not shown), but the overall effect was not significant.

Such studies would have to be extended through several wet and dry seasons to determine whether death of IHUs (or ramets) actually increases the chances of survival of the remaining ones, as postulated by Orshan (1972), or whether mortality of IHUs (or ramets) is completely independent. It appears likely that competitive interactions among IHUs occur mainly during resource pulses, and that they can indirectly affect the chances of survival during the inter-pulse periods, as suggested by Goldberg & Novoplansky (1997) for desert perennials in general.

Advantages of the clump growth form in deserts

The main reason that clonal desert shrubs have not received much attention is that fragmentation of most of these plants is not at all obvious to the observer, *Larrea tridentata* being a notable exception (Vasek 1980). Even highly fragmented genets often retain a dense clump growth form (Figure 1a). It appears that there may be advantages to such a growth form for desert plants that outweigh the potential advantages of a spreading growth form, such as reduced competition for light and possibilities of foraging for soil resources (Oborny & Cain 1997).

Clumped, intra- or interspecific spatial associations of desert plants are frequently observed, but here I will focus on the potential advantages for ramets to remain in close proximity instead of spreading out. Ramets may experience a more beneficial microclimate compared to that experienced by ramets that are separated by open spaces. In addition, shading and litter layers under clumps can reduce the amount of evaporation from the soil surface (Holzapfel & Mahall in press). Stemflow during rainfall can channel water deeply into the rooting zone of desert shrubs and thus minimize runoff (Martinez-Meza & Whitford 1996; West 1989). Long-lived clumps also affect other soil properties. For example, it has been found that hardpans (argillic horizons) under clumps are often partly dissolved, thereby sometimes creating a cup-shaped depression that can act as a water-reservoir (Bowns & West 1976; Wallace & Romney 1972; West 1989). The main advantage of long-lived clumps, however, may be the creation of fertility islands in the desert because such clumps accumulate litter and attract animals (Charley & West 1975; Garcia-Moya & McKell 1970; Garner & Steinberger 1989; Romney et al. 1977).

The advantages of a clumped growth form are apparently large enough to have made mono- and multi-specific clumps of plants an almost universal characteristic of arid and semi-arid environments. Some species even create clumps of closely related individuals by synaptospermous dispersal, so that several seeds from the same parent plant germinate in close vicinity. This is the case, for example, in the desert dwarf shrub *Rhanterium epapposum* (Asteraceae) in the sandy deserts of Iraq and Kuwait where several individuals often develop from the same flower head (Thalen 1979).

Conclusions and outlook

Clonal splitting in desert shrubs is a very common phenomenon that so far has received only scant attention from ecologists. We currently do not know exactly how widespread it is in plant families and geographical regions and whether it also occurs in shrubs from semi-arid or more mesic environments. The anatomical nature of the splitting mechanisms clearly suggests a connection to other structural forms of hydraulic segmentation. Further anatomical, developmental, physiological, and ecological studies are needed to determine whether axis splitting is in fact merely an extreme form of segmentation or whether there are other important aspects to this phenomenon.

This paper has only touched on some aspects of clonal splitting; there are certainly many others. For example, it would be interesting to know whether there is phenotypic plasticity in the formation and splitting of fluted axes and whether there are population- and/or habitat-specific differences within species. On a larger scale, one might ask whether axis splitting is restricted to certain evolutionary lineages, biogeographic regions, and/or environments. The most promising approach to test hypotheses and answer questions outlined in this paper would be to compare aspects ranging from anatomy and physiology to demography, community ecology, and biogeography of clonal splitters to those of aclonal shrubs in similar environments. It is to be hoped that the wish of Moss & Gorham (1953) reiterated by Ginzburg (1963), that 'further research (on axis splitting) may be stimulated' will finally come true.

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