Clonal integration of *Fragaria orientalis* driven by contrasting water availability between adjacent patches

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ABSTRACT. Experimental studies have shown that clonal plants can reciprocally translocate resources between interconnected ramets in heterogeneous environments. Resource contrast between patches in heterogeneous environments is the main external driver of integration effects. It was hypothesized that translocation of water between interconnected ramets was enhanced under higher levels of contrasts in water availability. A pot experiment with clonal fragments consisting of two interconnected ramets of *F. orientalis*—a stoloniferous herb widely distributed in China—was conducted. In the experiment, each of the ramets of the clonal fragments was allocated to either a high or low water treatment. The ramets in the high water treatment were maintained at 90% field capacity while those in the low water treatment were maintained at 90, 60 and 30% field capacity, respectively. The ramet developmental stage (proximal or distal from mother rosette) was accounted for by allocating either proximal or distal ramets in the contrasting patches. In order to assess the role of physiological integration among ramets, the stolon was severed for half of the clonal fragments. Stolon severing and drought stress had significant effects on plant performance, which increased with the increase of contrast. However, the directionality of stressed ramets had no influence on most treatments. Based on performance measures, a cost-benefit analysis showed that the dry ramets benefited from clonal integration at the cost of the connected wet ramets. The results indicated that this clonal species is able to withstand soil-water heterogeneity through physiological integration, which is promoted under increasing levels of water contrast. Our results suggest that clonal plants might be suitable for vegetation restoration in dry areas due to superior survival strategies.

Keywords: Clonal plant; Cost-benefit analysis; Drought stress; *Fragaria orientalis*; Heterogeneous environment; Physiological integration; Water transport.

INTRODUCTION

The resources for photosynthetic productivity such as light, soil water and mineral nutrients are often heterogeneously distributed in natural ecosystems (Frankland et al., 1963; Chazdon and Pearcy, 1991; Kelly and Canham, 1992; Ackerly and Bazzaz, 1995; Muraoka et al., 1997; Oshima et al., 1997). Resource heterogeneity usually occurs at different spatial and temporal scales and affects many ecologically important processes and phenomena, which can range from responses of populations (Wiens, 1976; Fowler, 1988; Levin, 1992), to individuals or parts of individuals (Shorrocks and Swingland, 1990; Caldwell and Pearcy, 1994).

Contrast is defined as the degree of difference between

patches or between a patch and its surrounding matrix (Kotliar and Wiens, 1990). The sink-source hypothesis states that photosynthetic rates may be regulated, at least in part, by the balance between source tissues (net exporters of photosynthates) and sink tissues (net consumers of carbohydrates) (King et al., 1967; Neales and Incoll, 1968; Sweet and Wareing, 1966; Wareing et al., 1968). For clonal plants, the contrast of patchiness, which is responsible for the establishment of source-sink relations between adult interconnected ramets (Marshall, 1990), plays a prominent role as the main external driver of integration effects (Stuefer, 1996). Many studies have reported that clonal plants in heterogeneous environments show a higher capacity for integration (Chen et al., 2004) and division of labor (Alpert and Stuefer, 1997; Roiloa et al., 2007).

Many species of plants are capable of clonal growth in natural communities (Oborny and Bartha, 1995; Klimeš et al., 1997). Clonal growth allows plants to form large systems consisting of a variable number of ramets located

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at some distance from each other, which remain connected by stolons or rhizomes for a variable period of time. This kind of reproduction implies that a clonal system in which ramets are connected by stolons or rhizomes is more likely to experience spatial heterogeneity than non-clonal plants (Roiloa and Retuerto, 2006b).

One of the most advantageous features of clonal plants is their capacity to exchange resources like water, photo-assimilates, and nutrients (Lau and Young, 1988; Alpert, 1991; D'Hertefeldt and Jónsdóttir, 1994; Lin et al., 2006; Wu et al., 2007; Hu et al., 2008) with non-resource agents-like defense compounds, signaling molecules, or patho-gens (Gómez and Stuefer, 2006) between interconnected ramets that are potentially independent (physiologically integrated). The advantages of physiological integration have been shown in a number of studies in which the connections among ramets were artificially severed and the impact on ramet performance measured (Mattheis et al., 1976; Hartnett and Bazzaz, 1983; Jónsdóttir and Cal-laghan, 1988; Schmid and Bazzaz, 1987; Schmid et al., 1988; Marshall and Anderson-Taylor, 1992; Bullock et al., 1994; Yu et al., 2004). Physiological integration is espe-cially advantageous when transport of resources is directed from old to young ramets (Hartnett and Bazzaz, 1983; Březina et al., 2006), from ramets in favorable microsites to ramets in adverse microsites (Alpert, 1991; Pennings and Callaway, 2000; Saitoh et al., 2002; Chen et al., 2004), or when reciprocal resources are shared between con-nected ramets of a clone in an environment where the two resources tend not to occur together (division of labor) (Roiloa et al., 2007). However, integration also has its disadvantages, such as the energy cost of maintenance for inter-ramet connections (Pitelka and Ashmun, 1985; Jóns-dóttir and Watson, 1997; Kelly, 1995) and the rapid spread of pathogens throughout the system of interconnected ra-mets (Stuefer et al., 2004).

Most previous experiments investigating integration in clonal plants in response to environmental heterogeneity have used only simple contrast models, such as contrast and no contrast, severed vs. unsevered stolon, and under shade or in the open (Salzman and Parker, 1985; De Kroon et al., 1996; Chen et al., 2004; Roiloa and Retuerto, 2006a). In natural environments, ramets of clonal plants often experience more complex habitats. However, little research has been done under these more realistic scenarios of habitat heterogeneity. Here, we add novel information by using a more complex system of heterogeneity with different levels of water contrasts.

In the transitional zone from the Qinghai-Tibetan Pla-teau to the Sichuan Basin, there is an ecotone between arid valley and montane ecosystems. The landscape of this kind of semi-arid area is characterized by vegetation consisting of scrubland, shrubland, and grassland (Liu, 1994), which provide suitable habitats for various clonal plants (Yu et al., 2002). Drought stress is an important environmental factor inhibiting plant growth and productivity (Li et al., 2000; Li and Wang, 2003; Yin et al., 2005). Clonal plants play important roles in the ecotone (Chen, 2004), and over many centuries, they have developed various mechanisms to enhance their drought adaptation (He et al., 2007). For example, the dry ramets of the *Carex* species get benefits from wet ramets through physical integration (De Kroon et al., 1996). Variation in mountainous terrain and nonunifor-mity of the vegetation cause heterogeneous distribution of water.

A pot experiment was used to test how the contrast be-tween adjacent patches affected the strength of clonal in-tegration in the stoloniferous herb *Fragaria orientalis*. In our study, the stolon between adjacent and connected sib-ling ramets was either severed or kept intact under differ-ent degrees of heterogeneous water supply treatment. We predicted that 1) drought would affect the growth and sur-vival of severed ramets of *F. orientalis*; 2) the integration between ramets of *F. orientalis* would be enhanced under higher levels of water contrast, and 3) under drought-stress the performance of ramets is different in proximal or distal ramets.

MATERIALS AND METHODS

Study site and plants

Our study was conducted in the Maoxian Ecological Station (31°41'07" N, 103°53'58" E; 1,816 m a.s.l.) of the Chinese Academy of Sciences in western Sichuan Prov-ince, P.R. China. The station is in an ecologically fragile region of the eastern Qinghai-Tibetan Plateau, located at the upper reaches of the Yangtze River. It has an annual mean temperature of 8.6°C, a mean annual precipitation of 919.5 mm, and an annual potential evaporation of 795.8 mm. The yearly sunshine duration is ca. 1139.8 h.

Fragaria orientalis Losinsk. (Rosaceae) is a stolonif-erous, perennial herb that is widely distributed in Korea, Mongolia, eastern Russia, and China. In China, it is com-mon in the north and in the eastern Qinghai-Tibet Plateau, inhabiting forests and meadows on mountain slopes (Yu et al., 1985; Guan et al., 2004). Stems and petioles are pilose (more densely in upper parts) or glabrescent. Leaves are composed of three leaflets with a slender petiole borne on the vertical stems with compressed nodes. The axillary buds on the vertical stems may grow out and form stolons. The stolons usually produce roots when reaching a moist substratum and often form a sympodial network of stolons above the ground. In the arid valley, variation in mountain-ous terrain and nonuniformity of vegetation cause hetero-geneous distribution of water. This spatial heterogeneity of water is characterized as patchiness, even on a small scale relevant to individual plants (Cook, 1983; Alpert and Mooney, 1986; Jackson and Caldwell, 1993). In this habi-tat, ramet systems of stoloniferous herb *F. orientalis* often experience patchiness of soil moisture. As growing in different patches, its interconnected ramets can transport and share water acquired by ramets in different patches due to clonal integration. So, *F. orientalis* provided proper materials for the experiment.

The experiment

On 10 June 2006, fifteen plants of *F. orientalis*, each consisting of more than twenty newly produced ramets, were excavated around the Maoxian Ecological Station. The plants were at least 1,000 m away from one another, and thus could be considered to represent fifteen distinct genotypes (Yu et al., 2002). All the second and third youngest ramets with connected stolon of these original plants were dissected into clonal fragments. One ramet in each fragment was designated the initial proximal part, indicating its relative proximity to the mother rosette, while the other was designated the initial distal part. With the stolon still intact between two ramets, these clonal fragments were planted in trays of sand for about three weeks. Once well established (rooted), they were size-standardized (Yu et al., 2002) and transplanted into plastic pots (20 cm in diameter and 15 cm in height). Each fragment was grown in a pair of plastic pots allowing for unsevered fragments to be connected by a stolon. Each pot was filled with homogenized soil to a depth of 14 cm. The proximal and the distal ramets of each clonal fragment were planted separately in adjacent pots, and they were connected by an undamaged stolon. Pots of severed clonal fragments were set up in the same procedure. The subjects were grown in a glasshouse under a semi-controlled environment, with a day temperature range of 12-31°C and a night temperature range of 9-15°C, and a relative humidity range of 35-85%. After one week, all ramets were size-standardized again so that ramets of a similar area remained. At the beginning of the experiment, all ramets were about 2 cm tall. The unsevered clonal fragments were divided into two groups: for one group, all the proximal ramets (wet ramets) were well-watered [up to 90% of field capacity (FC)], and the distal ramets (dry ramets) were subject to a well-watered treatment [90% of FC] and to two drought-stressed treatments (60% and 30% of FC). The other group was just the reverse, i.e., the distal ramets (wet ramets) were treated with 90% of FC while the proximal ramets (dry ramets) were treated with 90%, 60% and 30% of FC, respectively. Severed clonal fragments were treated in the same way. The experiment used a factorial design with different water level treatments (90%, 60% or 30% of FC), position of the stressed ramets (proximal or distal), and stolon severing treatment (severed or not) as main effects (Figure 1 and Table 1). In each treatment, there were fifteen replicates, and each of them was derived from one of the fifteen original rosettes. That is to say, each of the fifteen replicates came from a different one of the fifteen genotypes. A total of 150 pairs of ramets (10 levels of treatments × 15 replicates) were used in this experiment.

In the well-watered treatment, the pots were re-watered to 90% of FC by replacing the amount of water transpired every second day. In the drought-stressed treatments, the pots were watered to 60% and 30% of FC every second day to keep different drought levels in the soil. Evaporation from the soil surface was prevented by enclosing each pot with a plastic bag, which was sealed at the base of the stem of each ramet. A total of 8 g of slow-release fertilizer (13% N, 10% P and 14% K-Xinjin, Xinjin Compound Fertilizer Factory, Sichuan, China) was added to each pot before planting. An empirical relationship between plant fresh weight (Y, g) and plant leaf area (X, cm^2): Y = 0.096 X - 0.158 (R^2 = 0.923, P<0.001) was used to correct pot water for changes in plant biomass. In addition, 15 additional control pots were equipped with dry grass stems to model the evaporation situation with living *F. orientalis* and were enclosed in plastic bags in the same way as the ramets. These pots were also weighed every second day in order to estimate evaporation from the soil surface. At the end of the experiment, all parts of the plant in each pot were marked and harvested on 25 September.

Measurements and analysis

Total number of ramets and leaves per pot were counted. Total leaf area per pot was measured using a CI-203 Laser Area Meter (CID Inc.). The length of root, petiole and stolon of each ramet was measured. Every ramet was then dissected into roots, leaf laminaes, petioles, and stolons, and the biomass of each part was determined after drying at 70°C for 48 h.

A three-way ANOVA, with the main effects mentioned above, i.e., effect of severing, effect of water supply, and effect of directionality, was applied to analyze the responses of traits at the clonal fragment level and ramet level. Traits included biomass, number of ramets, height, root length, stolon length, leaf area, number of leaves, petiole
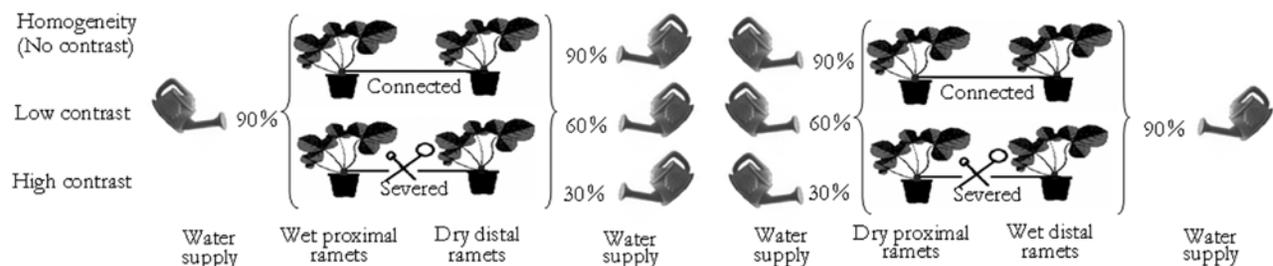

Figure 1. Schematic diagram of the experiment, showing different levels of water supply given to pairs of connected or severed ramets and proximal or distal ramets.

Table 1. Experimental design and survival of ramets.

Treatment	Wet ramets	Survival	Stolon connection	Dry ramets	Survival
Homogeneity	90% FC, proximal ramets	100%	Connected	90% FC, distal ramets	100%
(No contrast)	90% FC, proximal ramets	100%	Severed	90% FC, distal ramets	100%
Heterogeneity					
Low contrast	90% FC, proximal ramets	100%	Connected	60% FC, distal ramets	100%
	90% FC, proximal ramets	100%	Severed	60% FC, distal ramets	100%
	90% FC, distal ramets	100%	Connected	60% FC, proximal ramets	100%
	90% FC, distal ramets	100%	Severed	60% FC, proximal ramets	100%
High contrast	90% FC, proximal ramets	100%	Connected	30% FC, distal ramets	100%
	90% FC, proximal ramets	100%	Severed	30% FC, distal ramets	53%
	90% FC, distal ramets	100%	Connected	30% FC, proximal ramets	100%
	90% FC, distal ramets	100%	Severed	30% FC, proximal ramets	47%

Clonal fragment consisting of two successive ramets of *F. orientalis* were treated as two interconnected parts growing in two adjacent pots. The wet ramets were offered 90% FC, and the dry ramets were offered 90% FC, 60% FC and 30% FC. Half of the wet ramets and the dry ramets came from proximal ramets and the other half came from distal ramets. The stolon connection between the wet and the dry ramets of the same clonal fragment was either severed or not.

length, and root-shoot ratio. Duncan's multiple range test was employed to compare the means in all measured characters.

Costs and benefits of clonal integration were calculated separately for the dry ramets and the wet ramets in terms of biomass and number of ramets. Costs and benefits (Salzman and Parker, 1985; Slade and Hutchings, 1987a; Evans, 1991; van Kleunen and Stuefer, 1999; Yu et al., 2002) were defined as differences in biomass and number of ramets between interconnected ramets and the corresponding ramets in the severing treatment.

RESULTS

Effect of severing

At the end of the experiment, we found some of the severed dry ramets in the high contrast treatment had died, i.e., 53% of the distal ramets and 47% of the proximal ramets. All others survived (Table 1).

Stolon severing did not affect root-shoot ratio under homogeneity. The root-shoot ratio of dry ramets was significantly higher than that of wet ramets when they were connected, especially in high contrast. However, dry ramets and wet ramets showed no difference when they were severed. Under a heterogeneous water supply, the root-shoot ratio of connected wet ramets was higher than that of severed ones (Figure 2).

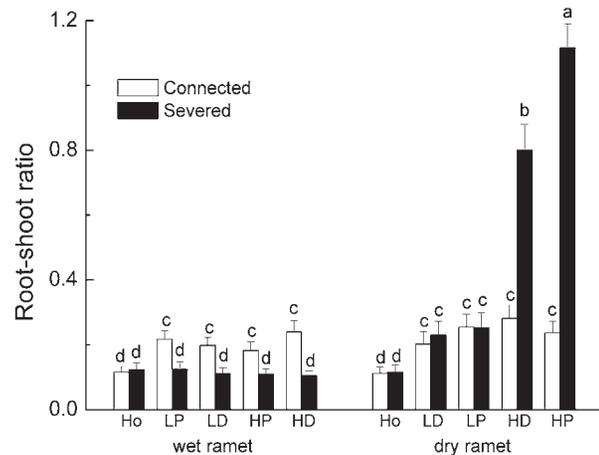Stolon severing increased significantly the biomass,

Figure 2. Root-shoot ratio. Ho, Homogeneity (no contrast); LP, proximal ramets under low contrast; LD, distal ramets under low contrast; HP, proximal ramets under high contrast; HD, distal ramets under high contrast. Filled bars show severed ramets. Empty bars show connected ramets. Error bars represent SE of the mean. Vertical bars sharing the same lowercase letter are not different at p=0.05.

number of ramets and petiole length of wet ramets and those of dry ramets under a homogeneous water supply. When stolons were severed, the biomass, height, and leaf area of dry ramets under a heterogeneous water supply decreased significantly, and the number of ramets, number of leaves, and stolon length of dry ramets under

high contrast also decreased significantly. When both ramets were in moist pots, severed fragments presented a higher biomass, more ramets and leaves, and greater root and stolon length, but lower height and petiole length in comparison with connected fragments. Severed fragments showed no difference in biomass, height, root length, stolon length, leaf area, or number of leaves in a heterogeneous water available environment (Figure 3).

Effect of water supply

No significant influence on root-shoot ratio was found among severed wet ramets. While for other ramets, root-shoot ratios under heterogeneous water supply were all bigger than those under homogeneous water supply. No significant differences were found either under low contrast or high contrast when wet ramets and dry ramets were connected, but root-shoot ratios of severed dry ramets increased with the increase of contrast (Figure 2).

Both biomass, number of ramets, leaf area, petiole length of dry ramets and height, number of leaves, stolon length of severed dry ramets decreased under heterogeneous water supply. The number of leaves and petiole length of connected dry ramets showed no significant difference between low contrast and homogeneous water supply, but a significant decrease was found under high contrast compared with homogeneous water supply. The biomass of dry ramets and number of ramets, leaf area, number of leaves, and stolon length of severed dry ramets decreased significantly with the increase of contrast. The biomass and leaf area of clonal fragments decreased under heterogeneous water supply (Figure 3).

Effect of directionality

Change of directionality showed no significant influences on connected ramets in the same water supply treatment (Figure 2). When stolons were connected, the biomass of dry proximal ramets was higher than that of dry distal ramets under low contrast, but there was no difference under high contrast. The parameters of connected ramets showed no differences under change of directionality except in the number of ramets and in the leaf area of wet ramets under a similar water supply. For the whole clonal fragment, significant differences were only found in the number of leaves of connected ramets under high contrast, and no differences were found on the other parameters of intact ramets (Figure 3).

Cost-benefit analysis

The cost-benefit analysis of biomass exhibited considerable benefits of clonal integration for dry ramets at the cost of wet ones, and such benefits increased with the increasing contrast between patches (Figure 3A).

The cost-benefit analysis in terms of the number of ramets also showed significant benefits of clonal integration for dry ramets at the cost of wet ones in high contrast, but the beneficial effect was less significant in conditions with lower water availability contrast (Figure 3B). The cost-benefit analysis of ramet livability also proved the benefits of clonal integration for dry ramets under high contrast (Table 1).

DISCUSSION

Thirty percent of FC showed markedly negative effects on the survival and growth of the severed ramets of *F. orientalis*. During the experiments, 53% of the distal ramets and 47% of the proximal ones among severed dry ramets in high contrast treatments died, indicating that drought was a major stress factor in the model environment, and that ramets in favorable habitats can provide support to drought-stressed ramets. Similar results were obtained for root-shoot ratio, biomass, number of ramets, height, leaf area, number of leaves, and petiole length. Thus, physiological integration between ramets of *F. orientalis* was beneficial for ramet establishment in patches with heterogeneous moisture. The effects of drought on *F. orientalis* was consistent with studies on other clonal species such as *Psammochloa villosa* (Dong and Alaten, 1999), *Carex hirta* and *C. flacca* (De Kroon et al., 1996), *Lycopodium flabelliforme* (Lau and Young, 1988), *Primula sieboldii* (Noda et al., 2004), *Potentilla anserina* (van Kleunen and Stuefer, 1999), *C. flacca* (de Kroon et al., 1998), *Distichlis spicata* (Alpert, 1990), *Pennisetum centrasiaticum* and *Leymus secalinus* (Ren et al., 1999), and *Hydrocotyle bonariensis* (Evans, 1991), where it was found that drought had negative effects on severed ramets, and the negative effects were ameliorated in connected ramets using a simple one contrast model. In our experiment, homogenous (no contrast) and low contrast treatment did not affect the survival of severed dry ramets, which showed that the benefits of clonal integration were different among various contrasts.

Under a heterogeneous water available environment, severed clones showed a higher root-shoot ratio for dry ramets but a lower one for wet ramets. However, the root-shoot ratios of connected clones showed no difference between dry and wet ramets. When the stolon between ramets was severed, each ramet was an independent plant, and its performance conformed to the classical theory of biomass allocation, which predicts an increase of biomass allocated to organs uptaking the limited resource. The dissimilar performance of connected clones was the result of a division of labor, at least in part, between dry and wet ramets (Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997). i.e. in order to easily uptake locally abundant water, more biomass was allocated to roots of wet ramets connected to dry ones under heterogeneous water supply, which made the root-shoot ratio of connected wet ramets higher than that of severed ones. Water of dry ramets was partly supplied from the root system of wet ones. This was inconsistent with the finding regarding *Cinnamomum tamala* and *Calamagrostis epigeios* (Zhang, 2002). Stolon severing had no appreciable influence on root-shoot ratio in a homogenous water available environment, which sug-
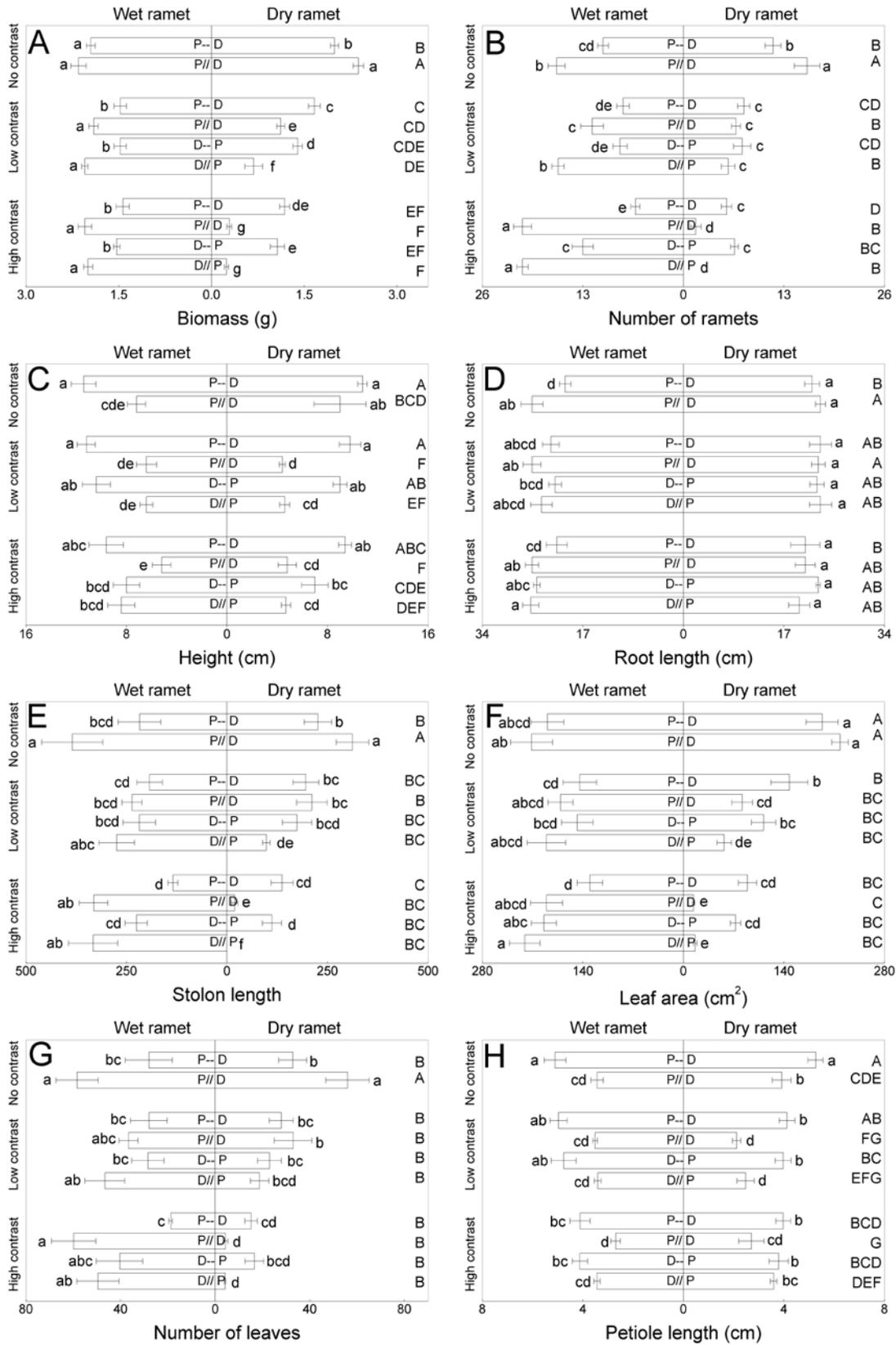
Figure 3. (A) Biomass, (B) Number of ramets, (C) height, (D) root length, (E) stolon length, (F) leaf area, (G) number of leaves, and (H) petiole length of the wet and the dry ramets. The letters on the bar: P, proximal ramets; D, distal ramets; --, connected stolon; //, severed stolon. Error bars represent SE of the means. The values for entire clonal fragments are the sum of those for the wet and the dry ramets. For the wet and the dry ramets, horizontal bars sharing the same lowercase letter are not different at p=0.05. Characters of the clonal fragments marked by the same capital letter are not different at p=0.05.

gested that there was equity in water exchange between ramets or that physiological integration did not occur when ramets were in the same water availability environment.

Severed fragments with both ramets in moist pots, severed dry ramets under homogeneous water supply and all wet ramets, had higher biomass, more ramets and leaves, and greater root and stolon length, but lower height and petiole length. This was inconsistent with a previous study of *Alternanthera philoxeroides* (Liu, 2005). Severed stolons eliminated the acropetal constraints on resource transport (Liu, 2005), which enhanced the growth of ramets as new individuals. In addition, severing gets rid of the energy cost of maintenance for inter-ramet connections (Caraco and Kelly, 1991). Severed ramets invested that energy in their vegetative growth. As for severed dry ramets under heterogeneity, their growth was inhibited by drought because there was no water supply from connected ramets.

As for contrasts of water availability, root-shoot ratios of severed dry ramets growing under high contrast were higher than those under low contrast, but no difference was found in contrast with connected dry ramets. A plausible explanation is that wet ramets provided more water to high contrast-treated ramets when they were connected. In other words, dry ramets gained more benefit from connected untreated ramets in high contrast, which slowed the increase of biomass allocated to organs uptaking water. In our experiment, the biomass and leaf area of clonal fragments, biomass, number of ramets, leaf area, petiole length of dry ramets and height, number of leaves, and stolon length of severed dry ramets decreased under heterogeneous water supply. This suggested that a decreased water supply affected growth of whole clonal fragments and dry ramets, especially severed dry ramets. The biomass and morphological responses of stressed ramets to drought were similar to those under other stresses such as shading (Slade and Hutchings, 1987a, b), nutrient depletion (Slade and Hutchings, 1987a, b; Evans, 1991), salinity (Evans and Whitney, 1992), or pathogen exposure (D'Hertefeldt and van der Putten, 1998). Neither the number of leaves nor the petiole length of connected dry ramets showed a significant difference between low contrast and homogeneous water supply, but a significant decrease was found under high contrast compared with homogeneous water supply. The biomass of dry ramets and number of ramets, leaf area, number of leaves, and stolon length of severed dry ramets decreased significantly with the increase of contrast. Those results indicate that integration between adjacent ramets is enhanced under higher water contrast. According to the sink-source hypothesis, water transport may be regulated by the balance between source tissues (water uptake tissues, such as roots) and sink tissues (transpiration tissues, such as leaves). In a clonal system, drought stressed ramets may behave like strong sinks and wet ramets like sources. For clonal plants, the contrast of patchiness played a prominent role as the main external driver of integration effects (Stuefer, 1996). Higher water

contrast increased the gap of source and sink. Thus, higher water contrast enhanced the integration between ramets of clonal plant.

Water transport was less influenced by directional constraints in plants because it was a passive process driven by water potential gradients, which arose from intra-clonal differences in water loss and water uptake (Marshall, 1990; Stuefer, 1996). Previous studies on *C. arenaria, C. flacca* and *C. hirta* also found that water translocation was equally effective in the acropetal (movement from the older to the younger part of the clone) and basipetal (movement from the younger to the older part of the clone) directions (De Kroon et al., 1996; D'Hertefeldt and Jónsdóttir, 1999). Tracer studies in *C. arenaria* and *Clintonia borealis* have shown that several clonal species assimilates are predominantly transported acropetally (towards developmentally younger clone parts), and to a much lesser extent in a basipetal direction (Pitelka and Ashmun, 1985; Marshall, 1990; D'Hertefeldt and Jónsdóttir, 1999). However, in *F. chiloensis* assimilates move in acropetal and basipetal directions (Alpert, 1996). In our study, transport of assimilates may be affected by both basipetal direction and water contrast. When stolons were connected, the biomass of dry proximal ramets was higher than that of dry distal ramets under low contrast, but it showed no difference under high contrast. This suggested that both basipetal direction and water contrast worked on assimilate transport in low contrast but water contrast predominantly worked on assimilate transport. Changing the direction of clonal fragments had no significant influence on most of the parameters for either whole fragments or ramets under the same water contrast treatments. A plausible explanation was that both of the ramets in the pair have become functionally independent, and therefore, transport that was driven by source-sink relations linked to development decreased. Transport was primarily driven by water contrast.

Translocation of substances to resource-deficient ramets potentially reduced the performance of the supplying part of a clonal fragment (Pitelka and Ashmun, 1985; Caraco and Kelly, 1991). Although integration for the supporting part of the clones has a cost, in general the benefits at a whole clone level outweigh it. When clonal fragments of *F. orientalis* were partially dry, and stolon connections between the dry and wet ramets remained intact, clonal integration conferred great benefits (in terms of biomass production and number of ramets) on the dry ramets (which presumably imported resources) and extracted significant cost from the connected wet ramets (which presumably exported resources). This contrasts with the results in *Ponteilla anserina* (Stuefer, 1995; van Kleunen and Stuefer, 1999) and *Hydrocotyle bonariensis* (Evans, 1991), which showed that clonal integration confers benefits on stressed ramets but no costs on the connected favored ramets. The reason wet ramets incurred no costs in the present experiment may be because ramets in a locally inferior environment can be helped by their neighbors but at some cost to

the contributing ramets (Salzman and Parker, 1985). De Kroon et al. (1996) showed that when a ramet pair of *C. flacca* or *C. hirta* was exposed to a heterogeneous water supply, water translocation strongly increased to a level at which 30-60% of the water acquired by the wet ramet was exported towards the dry ramet. Too much water export may affect the performance of donor ramets. An alternative explanation for the costs to exporting ramets can be that maintenance of tissues connecting ramets imposes metabolic costs (Pitelka and Ashmun, 1985) and vascular translocation may require an expenditure of energy (Epstein, 1972) affecting the growth of wet ramets. As a result of this positive cost-benefit balance, the ability of whole clonal fragments of *F. orientalis* to better cope with partial drought was greatly enhanced by the increase of dry ramet survival, especially in higher water availability contrast. Clonal integration can therefore be understood as part of a tolerance strategy that enhances the survival and growth of clonal plants growing in patchy environments (Grime, 1979; Pitelka and Ashmun, 1985). The clonal integration of *F. orientalis* can be appreciated as an adaptive strategy for the species.

It can be concluded from our findings that *F. orientalis* is able to withstand a heterogeneous distribution of available water, depending on physiological integration which would be enhanced under higher levels of water contrast. Furthermore, our results suggest clonal plants may be suitable for vegetation restoration in drought areas as they have superior survival strategies.

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異質生境斑塊間水分梯度對東方草莓克隆整合的影響

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　　生長在異質生境中的克隆植物分株間能進行物質傳遞，這種現象被稱為克隆整合。異質生境斑塊間的梯度是克隆整合的外在驅動力。我們假設克隆整合的強度隨斑塊梯度的增大而增強。文中我們用東方草莓兩個相連克隆片段的盆栽實驗驗證此假設。克隆片段被分為三組：無水分梯度組（高水分端 90% 田間持水量，低水分端 90% 田間持水量，30 個克隆片段）、中等水分梯度組（高水分端 90% 田間持水量，低水分端 60% 田間持水量，60 個克隆片段）、高水分梯度組（高水分端 90% 田間持水量，低水分端 30% 田間持水量，60 個克隆片段）。無水分梯度組中的高水分端均為克隆片段的近端分株，中、高水分組的高水分端一半為近端分株一半為遠端分株。將以上每種處理中一半克隆片段的分株間匍匐莖切斷、一半保留。實驗中乾旱脅迫和切斷匍匐莖對克隆分株有顯著影響，並且影響隨分株間水分梯度的增加而增大，但脅迫分株來自近端或遠端多數處理下沒有顯著差異。耗-益分析表明克隆整合中乾旱脅迫端分株受益但與其相連端生長受到抑制。實驗結果表明克隆植物東方草莓能通過分株間的克隆整合抵禦土壤水分異質性，並且克隆整合隨分株間土壤水分梯度的增大而增強。克隆植物對異質水分生境的這種適應性對乾旱地區的生態恢復具有重要意義。

關鍵詞：克隆植物；耗－益分析；乾旱脅迫；東方草莓；異質性環境；生理整合；水分傳輸。