Natural Science, 2016, 8, 475-486
http://www.scirp.org/journal/ns
ISSN Online: 2150-4105
ISSN Print: 2150-4091

Role of Clonal Integration among Different Environmental Conditions (A Review)

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How to cite this paper: Jaafry, W.H., Li, D.Z., Fatima, S.A. and Hassan, M. (2016) Role of Clonal Integration among Different Environmental Conditions (A Review). *Natural Science*, **8**, 475-486.
http://dx.doi.org/10.4236/ns.2016.811049

Received: August 17, 2016
Accepted: November 19, 2016
Published: November 22, 2016

Abstract

Most of the ecosystems are dominated by clonal species. The most unique feature of clonal plants is their capability for clonal integration (translocation of vital resources among connected ramets), implying that integration may play an essential role in their success. However, a general effect of clonal integration on plant performance is lacking. We conducted a text review on the effects of clonal integration on different habitats and species. Overall, clonal integration increased performance of clonal plants in different habitats. However clonal integration has also some limitations under stressful environments. Benefits of clonal integration may lack somehow when environmental stress increases. But connected ramets placed in unfavorable patches benefited more from integration compared to severed ramet placed in nutrient rich patches. Climate change and temperature increase have positive effects on biomass of clonal species.

Keywords

Clonal Integration, Habitats, Clonal Plants

1. Introduction

In natural environment many plant species acquire some extent of clonal growth named as "clonal plants" [1] [2]. In many ecosystems clonal plants are the core species and play a significant role in maintaining community organization and ecosystem functions [2] [3] [4]. The distinct ability of clonal plants to develop and reproduce themselves clonally had been a continuous interest for botanists. Thorough records of the morphology and composition of clonal plants exist from the middle of nineteenth century onwards. Afterward more research has targeted on the functionality of this interesting and complicated behaviour of modifying clonal plants to their local environment [5] [6] [7]. To explore deeply the distinct feature of clonal integration in clonal plants we decided to collect some closely relevant papers regarding clonal plants and review them for getting some new ideas and deficiencies in this field.

In terrestrial ecosystems, vital resources for plant conservation, growth and propagation, for instance nutrients, light and water, frequently are patchily dispersed in space and time [8] [9], even at levels admissible to plant individuals [10] [11] and its parts. Clonal plants escalate at right angel within the soil by virtue of stolons or rhizomes, and set up ramets in patches that may be different in resource inventory [10] [11]. Physiological integration can facilitate endurance and development of individual ramets endangered by opposition [12], grazing [4], environmental stress like wind erosion [13], sediment burial [14], salt stress [15], and light diminishing [16]. Development of younger ramets is facilitated by the flow of phloem and xylem contents from the older ramets to young ramet. By increment in age of younger ramet, the resource translocation from the parent ramet often declines, and the daughter ramets turn into self-regulating [17].

In natural habitats non-clonal plants frequently allocate additional resources to root system under low availability of soil nutrients to uptake more resources from the soil [18]. On contrary clonal plants adopt the reversed approach, by allocating additional resources to the growth of root organs placed within nutrient rich patches of soil [19] [20]. This strategy may enhance the overall performance of entire clone by translocating resources from source to sink (carbon, for example), and can be shared through ramets placed elsewhere. Main target of this review article is to explain the basic mechanism regarding clonal integration under different environmental conditions, and the limitations of clonal integration under different environmental stresses. The new ideas and research gaps still need to be explored in the field of ecology.

2. Role of Clonal Integration at Different Environmental Stress

Plants may adjust biomass allocation arrangement in response to the habitat [9]. Accessibility of soil nutrients is one of key factors that may determine resource allotment patterns [21]. One assumption is that plants in nutrient poor environments should allocate relatively more resources to roots to enhance their uptake capacity for these insufficient soil resources [8] [22]. Allocation of nutrient resources to different habitats has been the basic concept of life-history theory [11] [23], and allocation patterns mostly decide the capability of plants to detain resources, to contest with neighbours [24].

According to theoretical model of [25] in clonal plants clonal integration among connected ramets enhance entire growth and survivorship extensively more under heterogeneous than under homogeneous resource environment. One explanation for this may be clonal plants might be able to improve the efficiency of their resource consumption by distributing their resources along rhizome systems from more favorably placed nutrient rich ramets to ramets in less favorable micro-environments [26]. A further possible reason is that the resource acquirement of whole clonal fragments could be strengthen by raise up the photosynthetic capacity or resource uptake capacity in diverse environments (*i.e.* division of labor or plasticity behavior could be advantageous) [8] [27]. Many studies projected that clonal integration can encourage resource exploring performance, whereby a clone can utilize favorable nutrient rich patches or avoid unfavorable nutrient poor patches by the selective positioning of its ramets [25] [28].

Sharing of resources by means of clonal integration control survival, development, physiology and morphology of ramets, and as a result give benefits to the genet as a whole [29] [30]. Available nutrient and intensity of light are two essential plant resources that are frequently negatively associated in the field [29] [30]. The effect of clonal integration on plant performance may differ along with species and habitats [22] [31].

Soil conditions (soil nitrogen, available soil phosphorus and soil pH) had no effect on the biomass allocation of daughter ramet, in the *Black locust* when the ramets were remained interconnected. After severing of root connections, however, biomass allocation by the daughter ramets of black locust increased greatly in response to soil nitrogen and available phosphorus. Therefore, that result is inconsistent with the general behaviour of other clonal plants to response of soil heterogeneity [32].

All together, these results propose that in connected clones the nitrogen and phosphorus requirements of the daughter ramets are provided mainly by the (much superior) parent ramets during clonal integration. In these situations, daughter ramets are mostly insensitive to soil conditions. When the daughter ramet was detached from parent ramet, then, daughter ramets had no supply of nutrients by parent ramet so the younger ramet were required to allocate resources to root growth to get soil nutrients adequate to sustain growth, a behavior persistent with that of a non-clonal plant [18]. The variation among ramet size seems to be a key explanation of resource allocation. Well established parent ramet may easily share the nutrient requirement when young ramet is small. Conceivably morphological plasticity between interlinked ramets in response to nutrient rich patch has a selective benefit only when their size difference is comparatively small [32]. Nitrogen fixing shrubs that grow under the canopy of forest for example, soil nitrogen can be abundant but intensity of light may be low. On the contrary, in open field situations, availability of light is abundant but soil nutrients may be inadequate [33].

In these kinds of conditions, resource utilization by the genet can be better if individual ramets can take advantage of locally abundant resources by escalating growth in those organs valuable to resource uptake. For instance, by allocating more biomass to aboveground organs in segments of high light intensity, carbon can be fixed more by photosynthesis assuming that other potentially limiting resources can be translocated by ramets situated somewhere else. On the other hand, soil nutrient uptake can be enhanced by allocating more biomass to the root system of the plant located in patches with rich soil nutrient supply but low light intensity [14] [34] [35].

3. Role of Clonal Integration in Grazed Plants

Plant forage consequently leads to the reduction of photosynthetic tissue, however, which, most of the time outcome in a relative decrease of growth in herbaceous species [36] [37]. More often herbaceous plants are bared to different intensity of grazing.

In the study of Wang *et al.*, 2009, they found when rhizomes were connected size increased significantly, heavy clipping increased leaf and biomass density of both species *Bromus* and *Psammochloa* and also increased leaf and biomass density of *Psammochloa* under moderate clipping. Their results support that clonal integration has an essential role to indemnify the compensatory growth of clonal plants. Most probably this was due to one reason that clipped ramets picked up carbohydrates during clonal integration from their associated non clipped ramets, and as a result the adverse effects of clipping were extensively minimized. Under artificial herbivory clonal integration was also established to indemnify the unfavorable effects of defoliation on *Aster lanceolatus* and *Solidago canadensis* in old fields [38] and *Ipomoeapes-caprae* in beach dunes [39] (see **Table 1**).

Daughter ramets of invasive plant *Alternanthera philoxeroides* were also benefited from clonal integration by its mother ramet in response to artificial defoliation. Despite of defoliation intensity well established mother ramet translocated their resources to their interconnected daughter ramets to facilitate the growth of new tissues. This result was similar as the previous studies (from well-established older ramet to younger ramets) sharing of resources [13] [40] (**Table 1**). Many other invasive plants and *A. philoxeroides* promote the formation of young ramets and enhance the growth and clonal proliferation of young daughter ramet under stressful environments. These results specify that clonal integration may be significant in tolerating invasive clonal plants to discover more resources and may consequently raise their invasiveness in natural environments [41] [42].

Table 1. Role of clonal integration under defoliation.

Name of Species	Role of clonal integration due to defoliation	Remarks	Reference
Bromus ircutensis and *Psammochloa villosa*	Connected ramet significantly improved the performance *P. villosa* but no effect on Bromus	Moderate clipping did not reduce the biomass of both species, negative effects of heavy clipping were greatly mitigated in connected ramets	[65]
Alternanthera philoxeroides	Clonal integration increased maximum quantum yield F_v/F_m of daughter ramet under connected treatment	Due to clonal integration young ramet was supported by mother ramet regardless of defoliation intensity	[40]
Carex divisa Hude, Eleocharis palustris L., *Juncus articulatus* L., *Juncus gerardii* Lois and *Elytrigia repens* L.	The two species under experimental clipping (*E. palustris* and *J. gerardii*) shown best tolerance under grazing.	Reported to be found abundant in intensively grazed situations being grazed by macro-herbivores. *E. palustris* was shown to maintain the length of connections when defoliated and this fit well with its cover increase with grazing intensity	[66]
Caulerpa cylindracea	*C. cylindracea* cover increased by ~450% in 75% removal plots, ~200% in 50% removals and ~70% in 25% removals	in *C. cylindracea* by increase in clipping intensity the biomass also increased greatly	[67]
fern Diplopterygium glaucum	Survival rate was 100% in connected ramets and 27% survival in severed ramets	Clonal integration played vital role in connected ramets for their survival	[68]

4. Role of Clonal Integration Due to Climate Change in Wetlands

In estuarine habitats, many environmental factors may manipulate plant growth, existence, and competing interactions. Elements that may fluctuate geographically within wetlands include water depth, salinity level, flooding interval, SOM (soil organic matter), and sediment size of soil and nutrient abundance. Intraspecific variation in salt tolerance has been described in wetland herbaceous species [43] [44]. Among terrestrial ecosystems, the consequences of global warming on plant chemical reaction and growth can be changed by exposing with other environmental aspects, particularly root section moisture content of soil (Harte and Shaw, 1995; Sherry *et al.*, 2008) and available soil nutrient [7] [45] [46] (see **Table 2**).

Increase in average temperature globally may disturb plant population in many terrestrial ecosystems [46] [47] [48] [49]. By the last century, the average atmospheric temperature has elevated by 0.74˚C [50]. By the end of the 21st century it is expected in East Asia, that there would be increase in air temperature by 3.3˚C [51]. While climate change may generally enhance the biomass production of grass population [49], as a result of climate change the response is species specific according to their functional type (**Table 2**).

5. Role of Clonal Integration at Different Altitudes

Many environmental factor changes by increase in altitude, for example, lower temperature level higher solar radiation with higher exposure to the short wavelength radiations and lower atmospheric pressure. These factors create environmental stress more severe for growth of plants at higher altitude as compared to low altitude [52]. It has been reported that there is a higher extent of clonal integration in cold environment by using isotopic tracer analysis [53].

Alpine plants at high altitude, surviving in their origin with harsh winds, low temperature, exposure to high radiation levels and low fractional pressures of CO_2, have slow growing rate also in the common garden culture. These plants seem to be naturally

Table 2. Role of clonal integration in wetlands.

Name of species	Role of clonal integration in wetlands	Remarks	References
Spartina alterniflora	Biomass allocation was in controls or in shallow and deep water treatments were 119%, 108% and 149% higher than severed in old ramets	Clonal integration enhance the growth of *S. alterniflora* under flooding stress	[69]
Carex praeclara	By increase in sand burial intensity the mother ramet supported young ramet through increase in photosynthetic efficiency	With severing treatment biomass allocation was affected due to sand burial	[70]
Spartina alterniflora	At 5%, 20% and 35% substrate salinity level the growth and sexual reproduction decreased with increment in salinity level	Clonal integration very limited role on salinity and the growth and sexual reproduction of mother and daughter ramets	[71]
Scirpus mariqueter	Reciprocal translocation of resources were found in creekside communities within old and young ramets	In response to disturbance clonal integration may play a significant role	[72]

slow growing [52] [54]. Clonal integration is stronger at high altitude than low. At high altitude strong clonal integration seems to be more important in the perspective of ecology for the clonal plants that grow at higher altitude than lower habitats (**Table 3**).

According to Chen *et al*., 2004 overall effects of population on growth of the whole clonal section, for instance biomass, total stolon length and total number of ramets, were significant with increase in altitude. All of these factors were significantly higher for plants located at 3944 m above sea level (a.s.l.) than 1800 m (a.s.l.) Apart from altitude severing treatment had a negative impact on biomass and total stolon length of entire clonal fragments. When the ramets were remained connected the total stolon length increased significantly from two different altitudes, higher biomass and number of ramets for plants only from higher altitudes than lower [14].

Plants that grow under stressful environments most of the time have naturally low relative growth rate (RGR) comparatively to the plants which grow under favorable conditions [24]. Total biomass, total stolon length and number of ramets were significantly higher for plants at lower altitude 1800 m a.s.l. than from 3944 m a.s.l. It can be referred that plants at higher altitude have lower specific leaf area. According to patch scale higher resource sharing through clonal integration may lead to improved performance of whole clone [55] (see **Table 3**).

6. Clonal Invasions and Its Implications

Clonal growth has been repeatedly referred to as a characteristic that grants to plant invasiveness [56] [57] [58]. In fact, a substantial amount of the most invasive plant species globally having the ability of clonal growth [59]. The advantages of clonal plant species could have over non-clonal ones during invasion may comprise their capability to vegetative reproduction and tolerate in the deficiency of suitable pollinators and the ability to efficiently and rapidly cover a location through clonal growth [59] [60].

Although clonality is associated with invasiveness, most of the clonal plant species have not turn into invasive, and it is unidentified which behavior make some clonal species more invasive than others. Up till now, the mechanisms that clarify the dominancy of invasive species remain unclear [7] [61]. Some plant properties, such as clonal growth, could explain the success of invasive species [59] [62]. The knowledge about

Table 3. Clonal integration at different altitudes.

Name of species	Clonal integration at different altitudes	Remarks	References
Duchesnea indica	Benefit of clonal integration was observed more at high altitude than lower, *D. indica* was more responsive to severing treatment at high altitude	Clonal integration is more stronger at high altitude than low	[32]
Chara vulgaris	The effect of temperature increase the population of lower altitude were seem to be more tolerant than high altitude	Global warming will be negatively correlated with clonal integration at higher altitude than low	[73]
Fragaria vesca	Effect of clonal integration on two populations of *F. vesca* from different altitudes was same	However the performance of the whole clonal fragment seemed to be better at higher altitude than low	[14]

biological invasions is a quickly expanding field in ecology. Globally biological invasions characterize one of the most severe environmental threats, because non-native invasive species can alter the balance and functioning of native communities, and dislocate native plants with the subsequent loss of biodiversity [63].

In natural habitats, more often clonal plants are dominant species in terrestrial ecosystems, and have a significant role in the functioning of many plant communities and ecological units [64]. Main features related to clonal growth such as physiological integration, phenotypic plasticity, habitat selection and division of labor permit clonal plants to compete effectively in a wide range of habitats [27] [34]. In spite of that several of the most aggressive intrusive plant species execute clonal growth.

7. Conclusion and Future Recommendations

Role of clonal integration among the different habitats is species specific and its intensity varies in response to the degree of stress. In clonal plants there are many aspects of research which must be studied, we point out here a few of them. For further knowledge in the perspective of biodiversity more research should be conducted to control the biological invasion in cost effective way. Why some invasive species are more aggressive than other invasive clonal species? How does different soil pH affect clonal growth in different environmental condition? Furthermore, previous research has mainly focused on heterogeneous resource distribution where two resources are negatively correlated but significance of clonal integration in homogeneous resources is somewhat overlooked (but see Dong *et al.* 2015b; Zhang *et al.* 2016). Role of clonal integration should also be tested under different light regimes R and FR (red and far red light) intensities and its response of clonal species in forest understory. There is also no well-known research about clonal plant mutual facilitation mechanism, and how different kinship and siblings levels of seeds respond to the facilitation.

Acknowledgements

This study was supported by East China Normal University online library for downloading articles.

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