



CHICAGO JOURNALS



Facilitation within Species: A Possible Origin of Group-Selected Superorganisms.

Author(s): Eliot J. B. McIntire and Alex Fajardo

Source: *The American Naturalist*, Vol. 178, No. 1 (July 2011), pp. 88-97

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/660286>

Accessed: 16/06/2011 16:47

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=ucpress>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and The American Society of Naturalists are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

Facilitation within Species: A Possible Origin of Group-Selected Superorganisms

Eliot J. B. McIntire^{1,*} and Alex Fajardo²

1. Canada Research Chair—Conservation Biology, Département des Sciences du Bois et de la Forêt, Université Laval, Québec, Québec, Canada; 2. Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Bilbao 449, Coyhaique, Chile

Submitted October 31, 2010; Accepted March 18, 2011; Electronically published June 2, 2011

Dryad data: <http://dx.doi.org/10.5061/dryad.8869>.

ABSTRACT: Facilitation (positive interactions) has emerged as a dominant ecological mechanism in many ecosystems. Its importance has recently been expanded to include intraspecific interactions, creating the potential for higher-level natural selection within species. Using multiple lines of evidence, we show that conspecific facilitation within the southern beech tree, *Nothofagus pumilio*, appears to overcome competition in two life phases. In a seedling experiment addressing stress and planting-density effects, we found that mortality was lowest (~0%) where there was no stress and was indistinguishable across densities. Furthermore, in mature forests (45 years old), genetically variable, merged individuals had lower mortality (–50%) than unmerged individuals in locations without identifiable stress. Thus, a full understanding of the occurrence of facilitation may require a more general model of resource improvements than the commonly cited stress gradient hypothesis. Additionally, the merged trees showed a density-dependent mortality pattern at the level of the group. These data demonstrate a potential mechanism (facilitation) driving natural selection at this higher level, via stem merging. These merged “superorganisms” would confirm theoretical predictions whereby facilitation acts as an ecological mechanism driving group selection.

Keywords: multistemmed trees, *Nothofagus pumilio*, Patagonia, positive interactions, positive density dependence, stress gradient hypothesis.

Introduction

Positive, same trophic level interactions among organisms—often known as “facilitation”—have become formally included in community ecology theory (Bruno et al. 2003; Lortie et al. 2004a) and are known to increase local community diversity (Cavieres and Badano 2009). They are sufficiently well understood to affect conservation and restoration efforts (Gómez-Aparicio et al. 2004; Halpern et al. 2007), yet the evolutionary consequences of

facilitation have just begun to be explored (Brooker et al. 2008; Bronstein 2009; Kikvidze and Callaway 2009). In virtually all cases to date, facilitation has been observed and tested between unrelated species (Callaway 2007 and citations therein) or between individuals of the same species that are of dramatically different size (such as large individuals protecting small seedlings; e.g., Dickie et al. 2005; Fajardo et al. 2006; Eränen and Kozlov 2008). Consequently, there has been the implicit assumption that facilitation dominates where niche overlap is low or does not exist and that competition for common resources otherwise dominates. Thus, intraspecific facilitation is not expected to dominate in genetically unrelated individuals of the same cohort (Eränen and Kozlov 2008) because this condition would likely have the strongest resource-mediated competition.

A small set of studies, however, have shown intraspecific, same-cohort plant facilitation (Harley and Bertness 1996; Miller 1996; Bertness et al. 1998; Chu et al. 2008; Goldenheim et al. 2008; Fajardo and McIntire 2011). Although these previous studies laid some groundwork for conspecific facilitation (Fajardo and McIntire 2011), the special nature of intraspecific interactions was not explicitly addressed. First, facilitation becomes a population ecology phenomenon whose implications are not at all understood. Second, competition is supposed to be particularly strong among conspecifics of the same cohort (Silvertown and Charlesworth 2001). In trees, for example, forest-stand development in temperate latitudes has shown strong and ubiquitous competitive exclusion (Oliver 1981; Fajardo and McIntire 2007). Thus, numerous questions remain unanswered: Are there longer-term implications when conspecific facilitation occurs? Are the ecological conditions promoting facilitation within conspecific cohorts always the same as for other positive interactions? For example, does the stress gradient hypothesis (SGH; Bertness and Callaway 1994; Bruno et al. 2003; Callaway 2007; Brooker et al. 2008; Maestre et al. 2009), which states that

* Corresponding author; e-mail: eliot.mcintire@sbf.ulaval.ca.

the relative importance of facilitation increases with increasing abiotic stress, still hold? And do positive interactions among small individuals of the same cohort matter ecologically given that density-dependent mortality due to a lack of growing space eventually must act, thereby eliminating any earlier benefit?

Group selection—a “higher” level of the multilevel selection theory (Wilson and Sober 1994)—has a long history in the biological sciences (Williams 1966 and new preface in Williams 1996; Bell 1997; Keller 1999). Goodnight (2005) indicated that some key drivers of group selection are culture, behaviors enforcing conformity, shared diseases and symbionts, and changes in the local environment. An increasing number of studies over the past 15 years using contextual analysis have suggested that multilevel selection appears to be common in plants (e.g., Goodnight et al. 1992, 2000; Acosta et al. 1993; Stevens et al. 1995; Aspi et al. 2003). However, this higher-level selection has been demonstrated to occur via shared local environments (Goodnight 1985; Stevens et al. 1995; Aspi et al. 2003), not as the result of an emergent social (or “grouping”) trait, as is seen in some animals (Wilson and Wilson 2007). In other words, group selection in plants is now known to occur among a group of individuals that share similar genetically based traits because of their common environmental location (e.g., Weinig et al. 2007). Since plant facilitation is known to be a process that changes the local environment through the mitigation of limiting conditions (Callaway 2007), we propose that positive interactions can drive selection at a level above the individual, via changes to the local environment. This facilitation often involves physical proximity of individuals as the means of receiving the benefit, such as protection from high temperatures, wind abrasion, or snow scour—that is, the “nurse plant syndrome” (Callaway 1995; Kitzeberger et al. 2000). A priori, one would not expect selection for a local environmental feature at the level of the group because facilitation tends to produce a transient and extremely local change in the environment (Miriti 2006; Bronstein 2009) unless a heritable trait exists that can encourage facilitation.

A seemingly unrelated fact is that many plant species are known to be able to physically and physiologically merge (“grafting”) above- and belowground (Bormann 1966; Linhart and Tomback 1985; Fajardo and McIntire 2010; Tarroux and DesRochers 2010). This trait has long been used in agricultural applications (e.g., fruit trees; Hartmann et al. 1996) but with unknown ecological or evolutionary origins. While the implications of this grafting have been abundantly discussed (see the long discussions in both Graham and Bormann 1966 and Tarroux and DesRochers 2010) and the wide taxonomic occurrence has been described, merging has not, to our knowledge,

been related to any ecological condition promoting its occurrence or to a selective advantage for the trait.

Nothofagus pumilio (southern beech, Nothofagaceae) is a southern Andes broadleaf tree species that is dominant in Patagonian forests. We noted that this species forms multistemmed mature trees often at or near the outer edge of second-growth postfire forests, possibly of multiple-seed origin (Fajardo and McIntire 2010). Here, a multistemmed tree has a single stem at ground level with multiple vertical stems partway up the trunk (fig. 1). We previously demonstrated that the importance of facilitation increased monotonically across a purported stress gradient (a forest-prairie ecotone), supporting the SGH (Fajardo and McIntire 2011).

Our general objective is to understand the dynamics of *N. pumilio* forests by explaining the formation and consequences of these merged, intraspecific clusters. We ask specifically, is abiotic stress the driver of the mortality patterns in two different periods (during establishment and among mature trees)? First, we test the hypothesis that multistemmed mature clusters are of multiple genetic origins and are thus merged individuals, the relatedness of which is as-yet unknown. Second, we test the hypothesis that these merged individuals demonstrate facilitation as mature trees in addition to the known facilitation at the seedling stage. Third, we test the hypothesis that the individual stems in merged clusters overcome density-dependent mortality and act as if they were one stem, demonstrating not just physical contact but also physiological connections. With support for this final hypothesis, merged stems would scale up the natural selection process of stem exclusion (Oliver 1981) to the cluster, particularly once this is linked to the heritable group-level trait of merging.

Methods

Study Site Description

We selected second-growth single-tree-species forests of *Nothofagus pumilio* in Reserva Coyhaique (45°52'S, 72°00'W, 800 m above sea level on average), Coyhaique Province, Patagonia, Chile. In this particular reserve, a large-scale human-induced fire occurred around 1950 and burned some 600 ha of *N. pumilio* old-growth forest. The newly formed forest edge of old trees at that time became the likely source of seeds for the mature second-growth forest we studied here. This sequence of fire occurrence followed by the formation of a second-growth forest of *N. pumilio* is pervasive in this region (Quintanilla Pérez 2008; Fajardo and McIntire 2010). Unlike most other *Nothofagus* species, *N. pumilio* has no published occur-



Figure 1: Photograph showing an example of a merged multistemmed tree. This particular example was chosen because the tree is simultaneously in several phases of merging. The two closest stems appear to still have a gap between them, whereas the stems in the back of the cluster appear to have fully merged.

rence of vegetative sprouting outside alpine tree lines (Barrera et al. 2000).

*Seedling Experiment: Early Facilitation
and Planting Transect*

To determine whether abiotic stress is the driver of mortality patterns during the establishment period, we conducted a 3-year-long seedling experiment that has been described in detail elsewhere (Fajardo and McIntire 2011). In brief, we transplanted 2-year-old bare-root seedlings (10–15 cm tall) of *N. pumilio* into mammalian herbivore exclosure plots along four naturally occurring forest-prairie ecotones in March 2006 (i.e., late summer). At –30

m (inside closed forest), at 0 m (edge), and at 15, 30, and 50 m into the open prairie, we planted seedlings at two densities: dense clusters of 10 seedlings (planted as densely as physically possible, $265 \pm 11 \text{ m}^{-2}$ [$\pm \text{SD}$]) and isolated single seedlings. At each of the five distances, we planted two dense clusters and four single seedlings (total number seedlings = 480) at equally spaced grid intersections in a 2×3 -m rectangle. During each annual monitoring visit for the experiment, we assessed and confirmed that there was extremely little apparent herbivory by insect or vertebrate. At the beginning of the first growing season (October 2006), all seedlings were alive. A third-year census was conducted in March 2009, during which seedlings were recorded as being dead or alive. Light and wind levels

across the experimental gradient showed the expected increase in light and wind from forest to open prairie (Fajardo and McIntire 2011).

Mature Tree Study: Merging, Facilitation, and Selection

In the mature forest, we established four different edge plots and two interior plots (~1,500 m² each) where we mapped all live and dead stems (defined as each vertical stem at 1.35 m above the ground) >1 m tall ($N = 1,957$). In stem mapping, we estimated the coordinates of each stem center at breast height using a handheld laser range finder (Impulse) equipped with a digital compass (Laser Technology), which measures the horizontal distance and azimuth to each tree to the nearest 1 cm. The field measurements were converted to coordinates using trigonometric functions. The edge plots were located ~500 m from the unburned old forest and formed abrupt boundaries between the closed forest and open prairie habitats.

Genetic Analysis. To test the hypothesis that multistemmed trees have a multiple genetic origin, we sampled foliage from a haphazard selection of 30 mature trees ($N_{\text{ground,total}}$) located at the edge of the second-growth forest of fire origin, 15 of which were multistemmed and 15 of which were single stemmed (i.e., $N_{\text{ground,merged}} = N_{\text{single}} = 15$), and performed an analysis of amplified fragment length polymorphisms (AFLPs), a common technique for identifying individuals (Escaravage et al. 1998; Till-Bottraud et al. 2010). We collected foliar tissue from at least three stems (i.e., three vertical stems at 2 m above ground level; fig. 1) at each merged cluster ($N_{2\text{m,merged}} = 66$; $N_{2\text{m,total}} = N_{2\text{m,merged}} + N_{\text{single}} = 81$). Leaves were placed in labeled plastic bags with silica gel and sent to Laboratoire d'Ecologie Alpine, Université Joseph Fourier (Grenoble, France), for AFLP analysis. Total DNA was extracted using the DNeasy 96 plant-extraction kit (Qiagen), in accordance with the manufacturer's instructions. The AFLP procedure followed that of Vos et al. (1995) with minor modifications.

The AFLP profiles were scored using a semiautomated procedure to code the presence (1) or absence (0) of markers. Markers were defined manually with GENEMAPPER for the presence or absence of each marker in each individual. The quality of markers were then automatically checked with an R script (Herrmann et al. 2010) from within R software (R Development Core Team 2009). This script removes markers with a reproducibility smaller than 2% and screens phenotype identification (presence or absence of markers). AFLP fragments shorter than 50 base pairs were discarded. We included 35 duplicated samples to check the reliability of experiments. All markers with

more than one mismatch across the 35 duplicates were discarded. Finally, we developed a dendrogram of genetic distances calculated using the balanced minimum evolution algorithm (R project, package ape; Paradis et al. 2004) on the basis of the AFLP values.

Mortality. We recorded survival (alive or dead) of every mapped stem, merged and unmerged, in all six plots. The condition of being "dead" can last decades in these forests because wood decomposes slowly as a result of low temperature. To test whether abiotic stress is the driver of mortality patterns during the mature period and to test whether merged individuals have lower mortality rates than single trees, we compared survival among merged and single trees at the forest edge and in interior plots (see "Statistical Analysis"). Previous quantitative descriptions of our sites showed that multistemmed mature trees at these sites were more common at the edge of our second-growth forests of fire origin in the region but that age did not differ between merged and single trees. Density and basal area also did not differ between edge and interior sites (Fajardo and McIntire 2010). We knew, however, that diameter at breast height was 12% greater for live stems (14.6 cm) within a merged cluster than for live solitary stems (13.1 cm), although this was not a result of being at the edge per se (Fajardo and McIntire 2010).

Density Dependence. Using the stem-mapped plots, we calculated the nearest neighbor (NN) distance for each live stem (Diggle 2003) and compared these NN distances by merged status (merged vs. singles). To test the hypothesis that merged individuals are acting as single individuals in response to density-dependent mortality, we made three predictions (McIntire and Fajardo 2009). First, if density-dependent stand thinning occurs in even-aged forests, then NN distances will be larger around merged trees if the merged cluster is treated as a single stem because their aggregate basal areas will be very large (Kenkel 1988). Second, if these merged stems no longer act as separate individuals, then the NN distance will be smaller than expected compared with that for an isolated stem when they are treated as separate stems (in other words, they would be avoiding stem exclusion if they are abnormally large for their proximity). Third, if the spatial pattern of live and dead stems is due to density-dependent mortality rather than initial seedling patterns, then the nearest dead neighbor should be as close or closer to a live merged cluster than to a live single stem. The simultaneous occurrence of these three patterns supports the hypothesis that competition is occurring, creating space among stems, but that it is acting on the group as a whole, not on the individuals as separate entities.

Statistical Analysis

In all statistical analyses, we used mixed-effect regressions. For experimentally planted seedlings, we fitted the following logistic mixed model:

$$\begin{aligned} \text{logit}(N_{d,sp\theta} N_{a,sp\theta}) = & \beta_0 + \beta_1 L_{l,pt} + \beta_2 E_{sp\theta} \\ & + \beta_3 L_{l,pt} E_{sp\theta} + \alpha_p + \alpha_t + \varepsilon_{sp\theta} \end{aligned} \quad (1)$$

where the β are fixed-effect parameters to estimate; α_j are random effects to estimate; N is the abundance of dead, d , or alive, a , stems within each of s subplots, p plots, and t transects; L is the l dummy variable for location (0, 15, 30, and 50 m, with -30 m as the reference category contained within the intercept term) along the transect; E is the density of planting (high or low); ε is the error term; and $\text{logit}(\text{dead}, \text{alive})$ is the logit link used for binomial data of the number of dead “successes” and the number of alive “failures.” The sampling unit is the subplot (not the seedling), with either 1 or 10 seedlings. For mature tree survival, we fitted

$$\begin{aligned} \text{logit}(S_{kp}, 1 - S_{kp}) = & \beta_1 + \beta_2 T_{kp} \\ & + \beta_3 M_{kp} + \alpha_p + \varepsilon_{kp}, \end{aligned} \quad (2)$$

where S is survival status (dead or alive) within p plots, T is site type (either edge or interior), and M is merged status (merged or single). This analysis conforms to a simple contextual analysis (Heisler and Damuth 1987) in that it is a regression of a measure of fitness on an emergent trait (Goodnight 2005). We do not need to center our fitness measure (Goodnight 2005; Weinig et al. 2007) or the emergent trait because they are each binomial. Here, the sampling unit is the individual, k , in each plot. For NN distances, we fitted the following model with three different response variables:

$$\log(Q_{kp}) = \beta_1 + \beta_2 T_{kp} + \beta_3 M_{kp} + \alpha_p + \varepsilon_{kp}, \quad (3)$$

where Q is the NN distance between (1) each live stem with merged clusters treated as a single stem, (2) each live stem with merged clusters treated as multiple stems, or (3) each cluster or single stem and its closest dead stem. In regressions of mature trees (eqq. [2] and [3]), we included the site type to account for the variation resulting from being at an edge and thus to isolate the effect of being merged or single, which is the effect of interest. All analyses were done using R, with packages `lme4` (Bates and Maechler 2009) and `nlme` (Pinheiro et al. 2009).

Because of unbalanced designs, all means we report and illustrate are marginal means and SEMs from these linear models that take into account the other effects in the models (conducted using the `doBy` package; Højsgaard et al. 2009). To examine the significance of factors, we used the `anova` function in R, which performs an ANOVA (with

the F -test) for the linear model (eq. [3]) or a likelihood ratio test estimating a χ^2 statistic for all nested models within the two generalized linear models (eqq. [1] and [2]). Furthermore, for the experiment we were interested specifically in contrasts between low and high density at each given distance along the transect ($N = 5$), so we tested five planned contrasts: high versus low density at each distance along the transect.

Results

Seedling Experiment

Revisiting the seedling experiment (Fajardo and McIntire 2011), we found that the probability of mortality at the middle of the transect (i.e., the forest edge) was lowest for both solitary and densely planted seedlings (fig. 2). Furthermore, the probabilities were indistinguishable between densely planted seedlings (0.056) and solitary seedlings (0.022) after 3 years of growing.

Mature Trees

AFLP analysis indicated that the mean number of allele differences between any two pairs in the population (defined as single stems and a randomly sampled stem in each cluster) was 24.6 (SD = 6.0; fig. 3). Clusters were com-

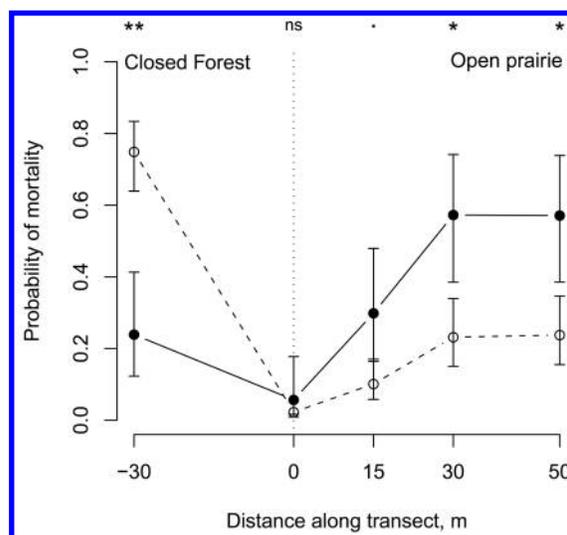


Figure 2: Probability of mortality (mean proportion \pm SEM from estimated model) of dense and solitary tree seedlings experimentally grown for 3 years across the forest-prairie ecotone. The solid line and filled circles represent solitary individuals, and the dashed line and open circles represent high-density individuals. Significance levels for planned comparisons between densities within a distance class are indicated at the top of the graph (*ns*, not significant; *single dot*, $P < .1$; *one asterisk*, $P < .05$; *two asterisks*, $P < .01$).

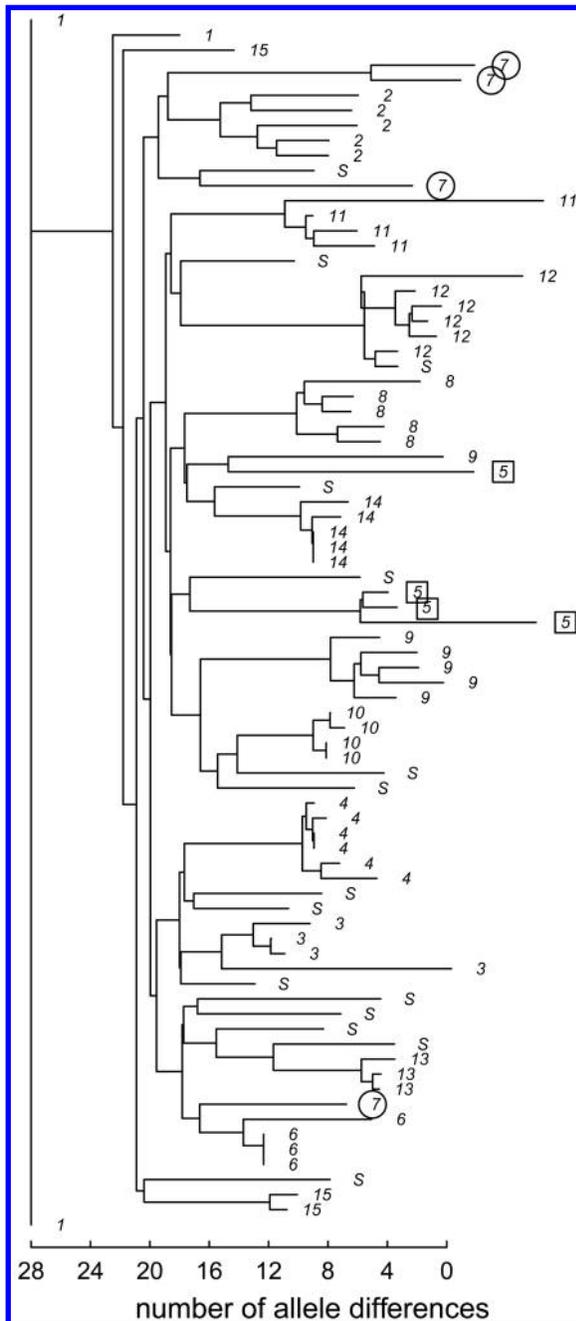


Figure 3: Dendrogram of genetic distances calculated using the balanced minimum evolution algorithm (R project, package *ape*; Paradis et al. 2004) on the basis of amplified fragment length polymorphisms. Each node end represents a single stem in either a solitary mature stem (S) or a multistemmed individual, where node ends sharing the same number indicate multiple members of a cluster. Two examples of clusters that include unrelated individuals are enclosed in squares (5) or circles (7). Genetic distances between individuals are represented by the length of the branch.

posed of many related individuals, but at least 7 of 15 multistemmed trees consisted of at least one stem that was either distantly related or not related to the other stems in the cluster (i.e., 3, 5, 7, 9, 11, 12, and 15). There was little evidence for vegetative origin of stems.

Mortality levels for single-stemmed trees (0.37 ± 0.06) were almost twice those for each stem in the merged clusters (0.19 ± 0.06 ; effect of status: $\chi_1^2 = 26.4$, $P < .001$; difference in Akaike Information Criterion [Δ AIC] for model with no effect of status: 24.4). This effect was not due to being at an edge per se (site type: $\chi_1^2 = 1.1$, $P = .29$), eliminating the possibility that the “edge effect” is the cause of the multistemmed benefits. Thus, survival is improved by being part of a group, not by being along an abiotic gradient of site type.

NN distances for each tree were much smaller among merged stems when treated as multiple stems than among single stems (fig. 4): single live stems had more than twice the NN distance (0.58 m) of merged live stems (0.29 m; $F_{1,144} = 113.1$, $P < .0001$; Δ AIC for model with no effect of status: 98.6). When we reran the analysis with multistemmed trees considered as if they were single individuals, NN distances from merged stems were much larger (1.45 m) than those from single stems (0.62 m; $F_{1,954} = 82.0$, $P < .0001$; Δ AIC for model with no effect of status: 72.8; fig. 4). In both cases, site type (edge or interior) did not have a significant effect on NN distances (merged as multiple stems: $F_{1,4} = 0.14$, $P = .72$; merged as single stems: $F_{1,4} = 0.667$, $P = .46$). The large vacant ring is consistent with the fivefold-larger basal area of the average group of merged stems compared with that of single stems (0.062 and $0.013 \text{ m}^2 \text{ m}^{-2}$, respectively). In the analysis of the nearest dead stem to each live cluster or single stem, no effect was significant (merged effect: $F_{1,954} = 0.64$, $P = .42$; site type: $F_{1,4} = 0.11$, $P = .75$). This indicates that the nearest dead stem was as close to each live cluster as to each live single stem. These results support the hypothesis that groups are acting like single trees. These patterns reject the alternative hypothesis that this intense clustering occurred randomly and was simply a consequence of close-growing seedlings.

Discussion

This study provides the first empirical evidence supporting the hypothesis that local, intraspecific positive interactions can have potential evolutionary effects at higher levels of organization (Kikvidze and Callaway 2009). This facilitation acts on groups of variably related individuals at least twice, through the merging of individual trees and with selection acting at the level of the group (sensu Goodnight 2005). The potential mechanism of the seedling facilitation appears to be consistent with the ubiquitous microhabitat

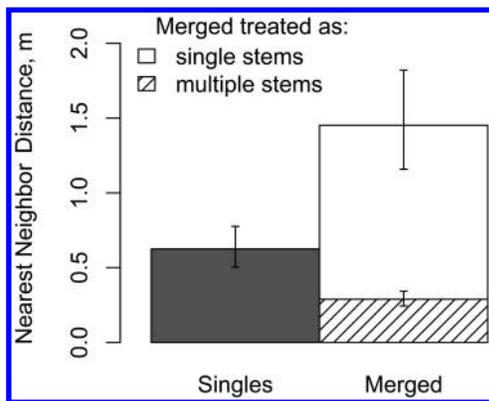


Figure 4: Nearest neighbor distances (mean \pm SEM from estimated model) for single stems, merged stems, and merged stems treated as single stems across six forest stands. Because we used marginal means and SEMs from estimated models, the marginal mean nearest neighbor distance for single stems is slightly different in the two models (0.59 and 0.62 m). See text for statistical tests.

amelioration and the SGH (e.g., Bertness and Callaway 1994; Callaway 2007; Maestre et al. 2009; Fajardo and McIntire 2011). However, the second period of facilitation appears to act through physical merging that is not tied to a stress gradient and that is demonstrated by the occurrence of merged mature trees of varied genetic origin that have lower mortality and better growth. With stand thinning causing mortality among these multistemmed trees as a group, we show that group selection via local environmental improvement is mediated by the plants themselves, possibly through resource sharing (Bormann 1966; Graham and Bormann 1966; Tarroux and DesRochers 2010).

Group Selection via Local Environmental Improvements

In many studies, strong inference in multilevel selection analysis has proceeded primarily using annual or short-lived plants in which lifetime fitness and heritability can be precisely measured (e.g., Lande and Arnold 1983; Goodnight 1985; Heisler and Damuth 1987; Swenson et al. 2000; Weinig et al. 2007). Here, we address the effect of the quantitative trait (merging) via its qualitative phenotypic expression (merged or not) on survival. This is a simple version of the contextual analysis with a single emergent group-level trait (Heisler and Damuth 1987) and with mortality as our surrogate of fitness. Because we do not quantify heritability, we cannot quantify the multigenerational aspect of this multilevel selection. We note that higher-level selection in plants is likely widespread because of differential environmental conditions (Goodnight 1985, 2000; Swenson et al. 2000). Unlike animals

(Wilson and Wilson 2007), plants are not thought to have the traits responsible for selection at the level of the group—that is, plants do not have culture or behaviors like those that can drive group selection in animals (Goodnight 2005). Because of the strong competition that would result, merging among conspecifics should not necessarily be an advantageous plant trait unless there is a major benefit for each individual. However, plants can and do improve their environment when growing in groups via facilitative interactions (Callaway 2007). Thus, any group-level trait that can promote the facilitative effects and that (1) varies, (2) is heritable, and (3) increases fitness could be selected at the group level (Lewontin 1970). Grafting is known to be variable and heritable, is regularly exploited in horticulture (Bormann 1966; Hartmann et al. 1996), and is widespread and genetically variable via root grafts in trees (Graham and Bormann 1966; Tarroux and DesRochers 2010). That innumerable woody species can physiologically merge suggests that the survival or growth benefits of merging may be very common. Our results support the hypothesis that facilitation is an ecological driver of group selection in plants.

Physiological merging should be a selectable trait that is more abundant and/or stronger in species in which positive intraspecific interactions occur. We show initial support here for this hypothesis. Temperate woody plants take up increasing amounts of growing space as they mature (Oliver 1981). Any individual benefits of growing in dense clusters as seedlings would be lost through lack of space (Oliver 1981; Kenkel 1988; Silvertown and Charlesworth 2001). However, any individual that has the ability to merge with neighbors would be more likely to survive the exclusion phase and would be able to pass that trait on to its progeny. The trait should likewise not be vulnerable to a parasitic strategy in which an individual takes resources but does not give back resources because the neighbors providing the benefits would die as a result of removing the positive interaction and survival benefit. Thus, parasitizing the strategy would reduce the fitness of the parasitizer. Finally, expression of the trait requires plants to germinate in a stressful location and to grow near other plants, both of which are common occurrences in many ecosystems. As we predict that merging should be more prevalent in woody species that have a higher probability of growing in relatively stressful environments, early successional tree species may be a good place to test this hypothesis further.

Facilitation Mechanisms: The Stress Gradient or Access to Resources?

We observed a valley in the pattern of absolute mortality across the gradient. This intermediate minimum mortality

is consistent with a plant response to two imperfectly correlated gradients and not with a single gradient. Because mortality is near zero at the edge, stress, defined as a factor that increases mortality (Lortie et al. 2004b), does not exist at the edge. Thus, the stress gradient occurs only from the edge outward into the prairie. In the forest, single seedlings do better, likely through competition for light; in the opening, groups do better, via facilitation (Fajardo and McIntire 2011). However, it is along both apparent gradients (i.e., from shade to open and from relatively moist to dry) that the mortality of the groups of densely planted seedlings decrease relative to that of solitary individuals. According to the SGH, the group curve in figure 2 should cross the solitary curve at a point to the right of zero stress at the edge.

Similarly, the lower mortality of the mature merged trees does not appear to be due to growing in stressful locations. A plausible mechanism for these benefits could be improved access to resources, a phenomenon observed when root grafts occur (Tarroux and DesRochers 2010). We do not know of another study that explicitly addresses facilitation among mature plants, and it may be that the SGH is primarily applicable to establishment and early growth. Since these additional potential mechanisms for facilitation may be most apparent among, but not limited to, conspecifics, we open up a novel area of research to understand what the effects of merging are and whether they are universally facilitative.

This study shows that there can be short- and long-term benefits in groups even when abiotic stress is minimal (Holmgren and Scheffer 2010). Positive interactions appear to overcome the costs of group selection for woody plants when merging occurs, producing what appear to be superorganisms (sensu Reeve and Hölldobler 2007) or supertrees. For this, aggregation of individuals would have to occur, and some sort of “social” behavior would likely be necessary. We have shown the former here and demonstrate that a well-known phenomenon (merging) would provide the necessary social mechanism.

Acknowledgments

Financial support for A.F. was received from the University of Montana (the CIEP-Montana project), the Chilean Fondo Nacional de Desarrollo Científico y Tecnológico (CONICYT; Proyecto de Fortalecimiento SS-2008-10), and the Universidad de Concepción (Semilla-Patagonia project 205.141.017-1sp) and for E.J.B.M. was received from the Natural Sciences and Engineering Research Council of Canada and the Canada Research Chair program. We thank the Corporación Nacional Forestal (CONAF) for facilitating access to Reserva Coyhaique and

for providing the seedlings for the transplanting experiment. We also thank I. Till-Bottraud (Université Joseph Fourier, Grenoble, France), who conducted the genetic analysis. Finally, we thank L. Cavieres, I. Till-Bottrand, and two anonymous reviewers for reading preliminary versions of the manuscript.

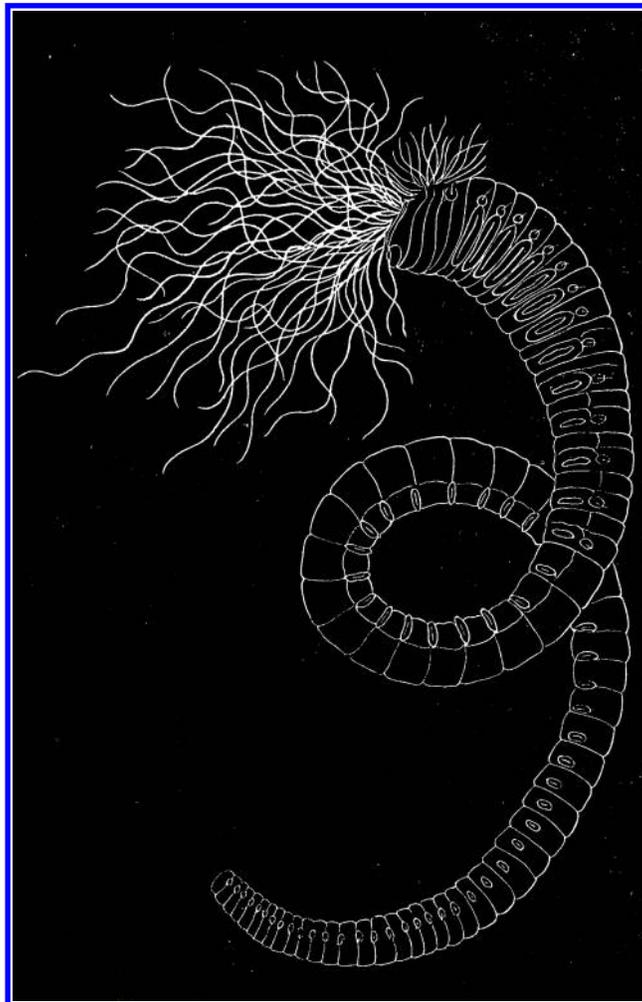
Literature Cited

- Acosta, F. J., J. M. Serrano, C. Pastor, and F. López. 1993. Significant potential levels of hierarchical phenotypic selection in a woody perennial plant, *Cistus ladanifer*. *Oikos* 68:267–272.
- Aspi, J., A. Jäkäläniemi, J. Tuomi, and P. Siikamäki. 2003. Multilevel phenotypic selection on morphological characters in a metapopulation of *Silene tatarica*. *Evolution* 57:509–517.
- Barrera, M. D., J. L. Frangi, L. L. Richter, M. H. Perdomo, and L. B. Pinedo. 2000. Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *Journal of Vegetation Science* 11:179–188.
- Bates, D., and M. Maechler. 2009. lme4: linear mixed-effects models using S4 classes. R package, version 0.999375-31. <http://cran.r-project.org/package=lme4>.
- Bell, G. 1997. *The basics of selection*. Chapman & Hall, New York.
- Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9:187–191.
- Bertness, M. D., S. D. Gaines, and S. M. Yeh. 1998. Making mountains out of barnacles: the dynamics of acorn barnacle hummocking. *Ecology* 79:1382–1394.
- Bormann, F. H. 1966. The structure, function, and ecological significance of root grafts in *Pinus strobus* L. *Ecological Monographs* 36:1–26.
- Bronstein, J. L. 2009. The evolution of facilitation and mutualism. *Journal of Ecology* 97:1160–1170.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. J. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119–125.
- Callaway, R. M. 1995. Positive interactions among plants. *Botanical Review* 61:306–349.
- . 2007. *Positive interactions and interdependence in plant communities*. Springer, Dordrecht.
- Cavieres, L. A., and E. I. Badano. 2009. Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology* 97:1181–1191.
- Chu, C.-J., F. T. Maestre, S. Xiao, J. Weiner, Y.-S. Wang, Z.-H. Duan, and G. Wang. 2008. Balance between facilitation and resource competition determines biomass-density relationships in plant populations. *Ecology Letters* 11:1189–1197.
- Dickie, I. A., S. A. Schnitzer, P. B. Reich, and S. E. Hobbie. 2005. Spatially disjunct effects of co-occurring competition and facilitation. *Ecology Letters* 8:1191–1200.
- Diggle, P. J. 2003. *Statistical analysis of spatial point patterns*. Oxford University Press, New York.
- Eränen, J. K., and M. V. Kozlov. 2008. Increasing intraspecific facilitation in exposed environments: consistent results from mountain

- birch populations in two subarctic stress gradients. *Oikos* 117: 1569–1577.
- Escaravage, N., S. Questiau, A. Pornon, B. Doche, and P. Taberlet. 1998. Clonal diversity in a *Rhododendron ferrugineum* L. (Ericaceae) population inferred from AFLP markers. *Molecular Ecology* 7:975–982.
- Fajardo, A., and E. J. B. McIntire. 2007. Distinguishing microsite and competition processes in tree growth dynamics: an a priori spatial modeling approach. *American Naturalist* 169:647–661.
- . 2010. Merged trees in second-growth, fire origin forests in Patagonia, Chile: positive spatial association patterns and their ecological implications. *American Journal of Botany* 97:1424–1430.
- . 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology* 99:642–650.
- Fajardo, A., J. M. Goodburn, and J. Graham. 2006. Spatial patterns of regeneration in managed uneven-aged ponderosa pine/Douglas-fir forests of western Montana, USA. *Forest Ecology and Management* 223:255–266.
- Goldenheim, W. M., A. D. Irving, and M. D. Bertness. 2008. Switching from negative to positive density-dependence among populations of a cobble beach plant. *Oecologia* (Berlin) 158:473–483.
- Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14:1128–1138.
- Goodnight, C. J. 1985. The influence of environmental variation on group and individual selection in a cress. *Evolution* 39:545–558.
- . 2000. Heritability at the ecosystem level. *Proceedings of the National Academy of Sciences of the USA* 97:9365.
- . 2005. Multilevel selection: the evolution of cooperation in non-kin groups. *Population Ecology* 47:3–12.
- Goodnight, C. J., J. M. Schwartz, and L. Stevens. 1992. Contextual analysis of models of group selection, soft selection, hard selection, and the evolution of altruism. *American Naturalist* 140:743–761.
- Graham, B. F., and F. H. Bormann. 1966. Natural root grafts. *Botanical Review* 32:255–292.
- Halpern, B. S., B. R. Silliman, J. D. Olden, J. P. Bruno, and M. D. Bertness. 2007. Incorporating positive interactions in aquatic restoration and conservation. *Frontiers in Ecology and the Environment* 5:153–160.
- Harley, C. D. G., and M. D. Bertness. 1996. Structural interdependence: an ecological consequence of morphological responses to crowding in marsh plants. *Functional Ecology* 10:654–661.
- Hartmann, H. T., D. E. Kester, F. T. Davies, and R. L. Geneve. 1996. *Plant propagation: principles and practices*. Prentice Hall, Upper Saddle River, NJ.
- Heisler, I. L., and J. Damuth. 1987. A method for analyzing selection in hierarchically structured populations. *American Naturalist* 130: 582–602.
- Herrmann, D., B. N. Poncet, S. Manel, D. Rioux, L. Gielly, P. Taberlet, and F. Gugerli. 2010. Selection criteria for scoring amplified fragment length polymorphisms (AFLPs) positively affect the reliability of population genetic parameter estimates. *Genome* 53:302–310.
- Højsgaard, S., K. Wright, and A. A. Leidi. 2009. doBy: groupwise computations of summary statistics, general linear contrasts and other utilities. R package, version 4.0.5. <http://cran.R-project.org/package=doBy>.
- Holmgren, M., and M. Scheffer. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology* 98:1269–1275.
- Keller, L. 1999. *Levels of selection in evolution*. Princeton University Press, Princeton, NJ.
- Kenkel, N. C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69:1017–1024.
- Kikvidze, Z., and R. M. Callaway. 2009. Ecological facilitation may drive major evolutionary transitions. *BioScience* 59:399–404.
- Kitzberger, T., D. F. Steinaker, and T. T. Veblen. 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* 81:1914–1924.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Lewontin, R. C. 1970. The units of selection. *Annual Review of Ecology and Systematics* 1:1–18.
- Linhart, Y. B., and D. F. Tomback. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. *Oecologia* (Berlin) 67: 107–110.
- Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire, and R. M. Callaway. 2004a. Rethinking plant community theory. *Oikos* 107:433–438.
- Lortie, C. J., R. W. Brooker, Z. Kikvidze, and R. M. Callaway. 2004b. The value of stress and limitation in an imperfect world: a reply to Körner. *Journal of Vegetation Science* 15:577–580.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97:199–205.
- McIntire, E. J. B., and A. Fajardo. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90:46–56.
- Miller, T. E. 1996. On quantifying the intensity of competition across gradients. *Ecology* 77:978–981.
- Miriti, M. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94:973–979.
- Oliver, C. D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management* 3:153–168.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analysis of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2009. nlme: linear and nonlinear mixed effects models. R package, version 3.1-92.
- Quintanilla Pérez, V. 2008. Perturbaciones a la vegetación nativa por grandes fuegos de 50 años atrás, en bosques Nordpatagónicos: caso de estudio en Chile Meridional. *Anales de Geografía* 28:85–104.
- R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. <http://www.R-project.org/>.
- Reeve, H. K., and B. Hölldobler. 2007. The emergence of a superorganism through intergroup competition. *Proceedings of the National Academy of Sciences of the USA* 104:9736–9740.
- Silvertown, J. W., and D. Charlesworth. 2001. *Introduction to plant population biology*. Blackwell Scientific, Oxford.
- Stevens, L., C. J. Goodnight, and S. Kalisz. 1995. Multilevel selection in natural populations of *Impatiens capensis*. *American Naturalist* 145:513–526.
- Swenson, W., D. S. Wilson, and R. Elias. 2000. Artificial ecosystem selection. *Proceedings of the National Academy of Sciences of the USA* 97:9110.

- Tarroux, E., and A. DesRochers. 2010. Frequency of root grafting in naturally and artificially regenerated stands of *Pinus banksiana*: influence of site characteristics. *Canadian Journal of Forest Research* 40:861–871.
- Till-Bottraud, I., B. N. Poncet, D. Rioux, and J. Girel. 2010. Spatial structure and clonal distribution of genotypes in the rare *Typha minima* Hoppe (Typhaceae) along a river system. *Botanica Helvetica* 120:53–62.
- Vos, P., R. Hogers, M. Bleeker, M. Reijans, T. van de Lee, M. Hornes, A. Frijters, et al. 1995. AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Research* 23:4407–4414.
- Weinig, C., J. A. Johnston, C. G. Willis, and J. N. Maloof. 2007. Antagonistic multilevel selection on size and architecture in variable density settings. *Evolution* 61:58–67.
- Williams, G. C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, NJ.
- . 1996. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, NJ.
- Wilson, D. S., and E. Sober. 1994. Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences* 17: 585–654.
- Wilson, D. S., and E. O. Wilson. 2007. Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology* 82:327–348.

Associate Editor: Tia-Lynn Ashman
 Editor: Judith L. Bronstein



“The *Amphitrite cirrata* is a curious tube-dweller. We have dredged it abundantly in the harbor of Eastport, Maine, that spot favored by fogs, cold storms, and icy sea-currents.” From “A Few Sea-Worms” by A. S. Packard Jr. (*American Naturalist*, 1868, 2:267–275).