PATTERNS OF RECRUITMENT AND YOUNG CULM MORPHOLOGY IN *ARUNDINARIA GIGANTEA* ([WALT.] MUHL.) CANEBRAKES IN WESTERN NORTH CAROLINA

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ABSTRACT

PATTERNS OF RECRUITMENT AND YOUNG CULM MORPHOLOGY IN *ARUNDINARIA GIGANTEA* ([WALT.] MUHL.) CANEBRAKES IN WESTERN NORTH CAROLINA

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River cane is one of three bamboos native to the United States. This species was once ubiquitous across the southeastern US but has now been reduced to less than two percent of its original coverage. This study is among research efforts to improve our knowledge to help restore a native species, protect riparian habitats, and improve materials needed for traditional Cherokee artisan crafts. The purpose of the project was to describe recruitment patterns within canebrakes, and to determine if these patterns were related to subsequent recruited culm morphology. Four canebrakes in western North Carolina were intensively sampled by establishing 1 m^2 plots every 3 m^2 across the entirety of each canebrake. All culms were counted within each plot and were categorized as young (recruited within 3 years) or old. Culm diameter, branch free height, and total height were measured for all young culms. Results showed young culms with larger diameters had greater branch free height and were taller, particularly after the first 3 m into a canebrake. This may be due to larger new rhizomes branching from older rhizomes, with the new rhizomes supporting new larger culms that can compete with pre-

existing culms for light. However, culm diameter, branch free height, and total height measures decreased in size in areas where there were greater than eight young culms/m^2, likely due to resource allocation trade-offs where greater recruitment occurred at the expense of culm size. The density of old and young culms had a patchy distribution within the canebrakes. This variation could be explained by clonal integration, which allows river cane culms in areas of high resources to continue to spread and support culms in resource poor areas. My results suggest creating thinned “gaps” in the interior of existing canebrakes could lead to production of larger sized culms if competition for resources is reduced and the older rhizomes support larger new rhizomes and greater competitive regeneration. Additionally, if canebrakes are allowed to expand in area so that greater interior area is created, overtime larger culms should be produced due to continual competition within the canebrake.

CHAPTER 1: INTRODUCTION

Arundinaria gigantea ([Walt.] Muhl.), commonly known as river cane or giant cane, is a perennial, monocotyledonous, woody grass (West 1934, Hughes 1951, Marsh 1977), and is one of three bamboo species native to the United States (Brantley and Platt 2001, Triplett et al. 2006). River cane has an expansive range across 22 states in the US; it extends from the New Jersey coast to Ohio, Texas, and the Florida coast (West 1934, Marsh 1977, Brantley & Platt 2001). River cane is primarily found in riparian areas from sea level to 600 m in the Appalachian Mountains (Marsh 1977, Farrelly 1984). Despite its expansive natural range, river cane has been reduced to less than two percent of its original coverage (Noss et al. 1995), largely due to anthropogenic causes such as urban development, agriculture, grazing, and water diversion (Brantley & Platt 2001). As a result of this habitat loss, over fifty species are threatened (Brantley and Platt 2001) including, Swainson's warbler (*Limnothlypis swainsonii* Audubon) that uses canebrakes for nesting, and six species of butterflies that are obligate bamboo specialists (Brantley and Platt 2001, Hunter et al. 2001). Conservation of river cane is also important for protecting water quality. Degradation and reduction of riparian areas such as canebrakes results in increased sediment movement into aquatic ecosystems (Sharpe et al. 2003). Datillo and Rhodes (2005) reported river cane functioned as well or better than forests as a riparian buffer, especially with sediment load reduction (Schoonover et al. 2005; 2006).

In addition to its ecological importance, loss of river cane makes it more difficult for modern artisans of the Eastern Band of Cherokee Indians in western North Carolina to find enough river cane with appropriate morphological qualities needed for their crafts.

Basket weaving requires culm diameters of approximately 2 cm and branch free heights of approximately 2 m (David Cozzo personal communication, August 2008). A 4x3 cm^2 basket can require 18-20 culms of cane (Hill 1996), and loss of river cane is limiting artisan production of traditional crafts made from traditional materials such as river cane.

Despite the importance of river cane, little is known about the patterns of regeneration and how these patterns might be related to regenerating (young) culm morphology. The objective of this study was to determine if recruitment and the young culm morphologic features including culm diameter, branch free height, and total height are related to canebrake density in western North Carolina. Improvement in our understanding of how recruitment and morphology are related to density could lead to the development of management practices that can promote regeneration of the quality of culms needed for Cherokee artisan use. Increased regeneration will also help maintain ecosystem functions provided by canebrakes.

CHAPTER 2: LITERATURE REVIEW

Bamboo Ecology

Bamboos are an important cultural and natural resource around the world (McClure 1966). They have been used as fodder for grazing in North America (Shepherd 1952), as musical instruments in many Asian countries, and as building materials for furniture and housing the world over (McClure 1966, Austin & Ueda 1978, Farrelly 1984). They are found on every continent except Antarctica, in tropical to temperate climates, and from sea level to the snow line (McClure 1966, Farrelly 1984). The bamboos are in the grass family Poaceae and are divided taxonomically between temperate and tropical bamboos (Triplett & Clark 2010). Bamboo groves (canebrakes) can be found as understory layers in various forest types and as the overstory in monotypic stands typical of river cane canebrakes (Farrelly 1984, Reid et al. 1991, Saitoh et al. 2002, Noguchi & Yoshida 2005).

Bamboos have seedling, vegetative, and sexual reproductive phases (McClure 1966, Farrelly 1984). In the sexual reproductive phase some bamboos, such as *Bambusa arundinacea* (Retz.) Willd. and several in the genus *Arundinaria*, flower once and die one to two years after flowering. Some bamboo species exhibit gregarious or mass flowering every year, but culms can also be sterile, or produce abundant fruit. Other bamboos flower periodically every 3 to 120 years (McClure 1966, Farrelly 1984, Austin & Ueda 1978). Growth and development in the seedling phase is poorly understood due to low amounts of viable seed to produce seedlings. The few seedlings produced can take 3-20 years to mature and produce rhizomes. Rhizome production initiates the vegetative phase.

However tillering, where additional new aerial stalks or culms grow from the base of the seedling, often occurs before the development of a rhizome. Tillering can also occur in mature culms, but this varies from species to species (McClure 1966, Marsh 1977).

Bamboos spend the majority or all of their mature life in the vegetative phase with new culms sprouting from constantly branching and spreading rhizomes (McClure 1966, Farrelly 1984, Liese 1998). A grove or canebrake forms in this clonally expanding phase where rhizomes become interwoven. Stand density increases, creating a monoculture of cane as the culms out-compete other vegetation. Canebrakes often consist of a single clone, termed a genet, though larger canebrakes may contain multiple genets. Canebrakes can increase in area in all directions as rhizomes spread out away from the periphery of the established stand and produce new culms (McClure 1966, Marsh 1977, Gagnon & Platt 2008). Bamboo species can be classified by the patterns of this vegetative growth as pachymorphic, leptomorphic, or a mix of the two patterns (McClure 1966, Farrelly 1984, Makita 1998). The pachymorph growth pattern is sympodial with clumps of culms growing close together, while the leptomorphic pattern is running or monopodial with individual culms spaced further apart. Makita (1998) noted some species such as *Sasa kurilensis* (Rupr.) Makino & Shib., exhibit a mix of leptomorphic and pachymorphic growth within the same genet.

Patterns of growth may be related to resources such as light, which has been documented affecting growth of bamboo culms (Li et al. 1998 a & c, Reid et al. 1991, Saitoh et al. 2002, Yue et al. 2004, Yu et al. 2006). For example, culm density and size of *Bashania fangiana* Yi, a leptomorphic understory species, is greater when overstory canopies are less dense and more light is available to the bamboo. However, completely open or completely closed canopies were associated with a reduction in size and density in *B. fangiana* (Reid et al. 1991). Taller culms tend to be more competitive because they capture more light (Reid et al. 1991). Taylor & Zisheng (1993) suggest that larger culms with their greater leaf biomass and height will out-compete neighboring smaller culms unless the smaller culms are connected to a common rhizome. In addition, allocation of resources between shoot and rhizome production can shift with light availability. For example, when light levels were high *Phyllostachys praecox* f. *prevernalis* produced greater numbers of new shoots but at lower light levels, rhizome lengths increased and more resources were allocated to height growth versus new shoot production. Yue et al. (2004) suggested this response allowed the bamboo to be more efficient at capturing light while also increasing the chance that new shoots will emerge in an area of higher light availability. Another bamboo species, *Fargesia nitida* (Mitford) Keng f. et Yi, also allocated more resources to leaf and rhizome growth at the expense of culm diameter and height under dense overstory canopies. Yu et al. (2006) suggest allocating biomass to leaves allows the bamboo to optimize light acquisition in low light environments. Similarly, larger leaves in *Sasa palmata* (Marlic) Nakai and maintenance of below ground biomass when above-ground height and diameter were reduced in low light conditions enable *S. palmata* to quickly take advantage of resources when they become available (Saitoh et al. 2002).

Clonal Integration

In addition to allocation of resources as a response to light, culms in a canebrake can be considered one entire organism; the culms obtain above-ground resources that are spread throughout the rhizome, which collects and stores below-ground resources to support new culm production and growth (McClure 1966, Farrelly 1984, Liese 1998). Translocation of resources from one culm to another allows a culm with access to abundant resources, such as light, to support a nearby culm with less access to resources (e.g. growing in the shade) (Taylor & Zisheng 1993, Makita 1996, Liese 1998, Saitoh et al. 2002). Even where resources are more evenly distributed, new culms can benefit from translocation of resources from older culms. In the leptomorphic giant bamboo *Phyllostachys pubescens* (Mazel) Ohwi, translocation of resources (Liese 1998) increased the survival of new shoots, particularly those closer to a parent culm (Li et al. 1998 a & b), with survival related to the amount of resources that can be translocated by the parent shoot (Li et al. 1998a). Saitoh et al. (2002) found that although density and size of *S. palmata* daughter ramets were less in the shade compare to full sun, the decrease was less when daughter ramets were connected to a parent ramet who had access to light.

This translocation of resources in clonal plants such as bamboos occurs through physiological (clonal) integration (Harper 1977). This clonal integration can modify density dependent characteristics (Hutchings 1979, Hartnett & Bazzaz 1985). For example, when grown at high densities from seed, leaf total, biomass, and reproduction declined in the clonal plant *Solidago canadensis* L. However, with integration these density dependent responses were reduced suggesting that integration makes ramets less sensitive to within-species competition (Hartnett & Bazzaz 1985). Clonal integration can also affect self-thinning by allowing clonal plants to reach and maintain stand densities higher than what self-thinning would allow (Hutchings 1979). Since self-thinning is normally driven by competition for resources, the ability of clonal plants to share assimilates reduces competition effects (Harper 1977, Hutchings 1979, Silvertown 1987). Clonal integration allows clonal plants to maintain dominance of a habitat and increase in biomass over time.

Other research indicates that clonal integration does not affect density when recruitment is regulated by individual ramet competition, and this may vary by plant species (Briske & Butler 1989, DeKroon & Kwant 1991). Areas of high density in *B. fangiana* (Taylor & Zisheng 1993) and *Sasa tsuboiana* Makino (Makita 1996) had fewer newly regenerated culms. However, *S. tsuboiana* produced greater numbers of smaller culms until it reached a density full state. Then self-thinning began, where fewer but larger culms were produced (Makita 1996).

In addition to translocation of photosynthates, clonal integration allows the sharing of resources such as water and nitrogen, thus improving growth and survival (Hartnett & Bazzaz 1983, Alpert & Mooney 1986, Evans 1992, Wijesinghe & Handel 1994). Hartnett & Bazzaz (1983) reported daughter ramets of the herb *Solidago canadensis* L severed from their mother ramets had decreased growth, survival, and flowering. They concluded the daughter ramets depended on translocated resources from the mother ramet, especially during early growth. Although this dependency diminished over time, when resources became limiting the daughter ramet could re-integrate with the parent as long as the connection remained (Hartnett & Bazzaz 1983). Resources generally move from mother to daughter ramet (Slade & Hutchings 1987d), but the reverse can occur in some species such as *Fragaria chiloensis* (L.) Duchesne (Alpert 1991). In addition, morphology of ramets of *Hydrocotyle bonariensis* (Apiaceae) depend on the resource being translocated. Leaf characteristics such as blade area were larger in the shade, while translocation of water and nitrogen generally increased clonal spread and flowering (Evans 1992).

Although, clonal integration can improve survival, individual ramet growth is not always increased. For example, clonal integration in *F. chiloensis* results in increased vegetative expansion rather than increased biomass of individual ramets (Alpert 1999). Clonal integration allows expansion and survival of ramets into environments where resource availability changes with seasons or is patchy (Hartnett & Bazzaz 1983, Alpert & Mooney 1986, Evans 1992, Wijesinghe & Handel 1994). Wijesinghe & Handel (1994) found intact ramets of *Potentilla simplex* Michx. (Rosaceae) had greater biomass weight than disconnected ramets in heterogeneous habitats, and that increasing resource patchiness increased the benefits of being interconnected. Slade & Hutchings (1987a) reported ramets of *Glechoma hederacea* L. (Labiatae) in nutrient rich plots consolidated growth by creating many ramets with larger leaves, and shorter stolons. Ramets in nutrient poor plots had reduced biomass but increased stolon length, which has also been seen in other species (Salzman 1985). Ramets in a split nutrient-rich and nutrient-deficient plot exhibited an intermediate amount of growth, suggesting that plasticity of growth and integration help to support the herb’s expansion (Slade & Hutchings 1987a). Many clonal species have more branches under favorable conditions such as increased water or light availability, but rhizomes and stolons respond more variably, and in some species there is no significant response. DeKroon & Hutchings (1995) suggest that variation in biomass and root size is due to plasticity, which enables exploitation of high concentrations of resources. Variation in rhizome and stolon length is likely indicative of random continual searching.

In summary, clonal integration allows translocation of resources between plants and increases survival in heterogeneous environments. Resources can be allocated to increase biomass or to increase expansion, depending on environmental conditions. Additionally, density dependency in clonal plants can be modified by clonal integration as seen in some bamboo species, where new culm density can increase to a high level before intra-specific competition causes self-thinning to occur. This allows clonal plants and bamboos to maintain dominance and when combined with morphological plasticity, allows them to take advantage of heterogeneous environments.

River Cane Ecology

River cane appears to be a generalist, enabling it to succeed in multiple habitat types, though the rooting zone needs to be out of the zone of saturation (Dunbar 1789 as cited in West 1934, Marsh 1977, Griffith et al. 2009). Well-drained sandy soils with low bulk density support the best river cane growth and canebrake expansion. River cane has been shown to be highly drought resistant as well as able to tolerate a wide range of nitrogen levels (Cirtain 2004, Griffith et al. 2009, Osland et al. 2009).

River cane can reproduce sexually but similarly to other bamboos, the seeds have shown poor viability (Hughes 1951, Marsh 1977, Baldwin et al. 2009). The best seed germination rates occur in dark, moist, but well drained conditions (Neal et al. 2010). Most fertile culms belong to a single clone, however, not all culms of the same clone flower (Mathews et al. 2009). Although some river cane can persist after flowering, the species is generally monocarpic, meaning that culms flower once and die, thus creating openings for new seedlings to establish (Marsh 1977). Over time these openings fill in with new culms from the established rhizomes (Marsh 1977). As a result most river cane canebrakes consist of one genet (Mathews et al. 2009).

River cane rhizomes are leptomorphic and have been observed to grow 6 m in a season. Rhizomes continue to grow horizontally from the rhizome apex (tip) in successive seasons, though some will turn up vertically and become a terminal culm (West 1934, McClure 1966, Marsh 1977, Makita 1998). The lifespan of a rhizome and whether every rhizome apex becomes a terminal culm is unknown. As with other bamboos, the nodes of the rhizome have lateral buds, which can become either a new culm or a new rhizome (McClure 1966, Marsh 1977, Farrelly 1984, Liese 1998). Like most bamboos, river cane rhizome diameters are fixed, but over successive seasons, new growth can be greater in diameter than the rhizome from which it grows or branches, usually at acute angles in river cane (West 1934, McClure 1966, Marsh 1977, Farrelly 1984). Rhizome diameter is related to the age of the canebrake and habitat conditions such as soil bulk density or overstory tree species, whose roots affect soil bulk density, moisture availability, and soil pH (West 1934, Marsh 1977, Crozier & Boerner 1984). River cane rhizome diameters are greater in loose, well-drained soils compared to compact soil (West 1934, Marsh 1977, Cirtain 2004, Griffith et al. 2009).

New culms typically appear beginning in the spring and continuing through early fall. New culms emerge as "mutton cane" or soft culms from nodes along the rhizomes (West 1934, Hughes 1951, Marsh 1977) at intervals of 0.5 meters or less along the same rhizome (Marsh 1977). Culms have been observed to increase in height by as much as 4 cm in a 24-hour period (Meanley 1972, Hill 1996), reaching their maximum heights within a few weeks of emerging, then becoming "woody". A modified leaf, or sheath, protects and supports the soft meristematic tissues of culm internodes until culms harden. These sheaths dry and fall off as the environment weathers them, or when branches emerge. Lateral branches can grow from buds on nodes of culms that emerged early in the growing season, but branches will not be produced until the beginning of the next growing season on culms that emerged later in the season (West 1934, McClure 1966, Marsh 1977). A culm is generally considered mature after it has hardened and formed lateral branches; culms without sheaths are generally older than those with culm sheaths. The lifespan of a culm has been reported to vary from one to over five years with culm diameter and height at maturity varying greatly from 3 - 25 mm and from a few centimeters to greater than 9 m, respectively (Hughes 1951, Marsh 1977). The apical bud of the culm ceases to function after the first growing season and there is limited intercalary culm growth. Therefore as with other bamboos, culm diameter is fixed at emergence and once maximum height is reached, the only growth in successive seasons is more branches (West 1934, McClure 1966, Marsh 1977, Liese 1998). Both genetics (Berndecke 2008, Zaczek et al. 2009) and environmental factors appear to influence maximum height.

Studies of large canebrakes have suggested that forest canopy cover and surrounding culms can cause newly emerging culms competing for light to be taller than their surrounding neighbors with each successive season (West 1934, Marsh 1977, Gagnon et al. 2007). However, this pattern has not been consistently observed in smaller stands (Marsh 1977). The diameter of a culm is typically equal to or slightly greater than that of the rhizome from which it emerged. Culms in younger canebrakes have lateral buds at all the nodes. Culms in older canebrakes have lower nodes free of buds, and are usually taller with half of their height free of branches (West 1934, Marsh 1977). Culm morphology also varies with position within a canebrake. New culms along edges and regenerating in gaps tend to be shorter in height and smaller in diameter than culms emerging within a canebrake (West 1934, Hughes 1951, Marsh 1977, Gagnon et al. 2007). Cirtain et al. (2009) and Gagnon et al. (2007) reported greater sizes of new shoots when more light was available.

In addition to potential relationships between light and culm morphology, river cane regeneration appears to be related to increased light availability such as created by gaps (Marsh 1977, Gagnon et al. 2007, Cirtain et al. 2009, Osland et al. 2009). Gagnon et al. (2007) found less regeneration within the interior of a canebrake compared to gaps and Cirtain et al. (2009) reported greater numbers of culm shoots when the overstory canopy was thinned. Gagnon & Platt (2008) reported a rapid doubling of ramet density in openings created by the combination of fire and wind as opposed to either disturbance alone. However, others (Hughes 1951, Shepherd 1952, Marsh 1977) found that if these types of disturbances occurred too often, regenerating culms were smaller and it took many growing seasons for the canebrake to consist of large sized culms.

In summary, the studies reported above suggest that river cane regeneration occurs primarily in gaps and along the edges, and less so within the interior. However, regeneration patterns across canebrakes have not been quantified. While the morphology of regenerating culms has been observed, the correlation between any one characteristic and their location within a canebrake also has not been thoroughly tested.

CHAPTER 3: MANUSCRIPT

Introduction

River cane, *Arundinaria gigantea* ([Walt.] Mull.) is one of three species of bamboos native to the United States (Marsh 1977, Brantley & Platt 2001, Triplett et al. 2006). River cane's native range includes 22 states in the south and eastern United States, primarily in riparian areas where dense, generally monotypic patches called canebrakes occur (West 1934, Marsh 1977, Brantley & Platt 2001). River cane has been reduced to less than two percent of its original cover in its native range largely due to anthropogenic causes such as urban development, agriculture, grazing, and water diversion (Noss et al. 1995, Brantley & Platt 2001). Canebrakes in western North Carolina range from small clumps of culms that have been mowed repeatedly to more extensive and generally linear canebrakes that have persisted up to 15 years or more. Canebrakes can be found as the overstory in monotypic stands or as the understory in association with various riparian tree species such as red maple *(Acer rubrum* L.*),* dogwood *(Cornus florida* L.*),* black locust (*Robinia pseudoacacia* L.), black walnut (*Juglans nigra* L.), sycamore (*Platanus occidentalis* L.*)*, and ironwood (*Carpinus caroliniana* Walter) (Griffith & McDowell 2008).

River cane is an evergreen, perennial woody grass (West 1938, Hughes 1951) that is a leptomorphic or spreading bamboo (McClure 1966, Marsh 1977). Regeneration occurs primarily by vegetative sprouting from the rhizomes along edges of canebrakes (West 1934, Marsh 1977, Gagnon & Platt 2008). However, regeneration can also occur within canebrake interiors where density of existing culms tends to increase over time, and typically varies from 5-34 culms/m^2 (Marsh 1977, Blattel et al. 2005, Gagnon et al. 2007). Disturbances, such as fire or flood that create openings within canebrake interiors, promote regeneration and growth by reducing competition (Hughes 1951, Marsh 1977, Brantley & Platt 2001). Large-scale disturbances, such as both tornado and fire, can increase clonal regeneration nearly two fold (Gagnon et al. 2007, Gagnon & Platt 2008), but too frequent disturbance can result in smaller sized cane and tillering (West 1934, Hughes 1951, Marsh 1977). Tillering produces new culms that arise from the base of old culms instead of the rhizomes (McClure 1966, Marsh 1977).

The apparent relationships in river cane between disturbance, regeneration, and growth may be density dependent responses (Harper 1977). This is similar to responses in the leptomorphic bamboo *Bashania fangiana* ([A. Camus] Yi), where less regeneration occurred in areas of higher mature culm densities (Taylor & Zisheng 1993). Lower densities that reduce culm-to-culm competition and thus promote regeneration also explain the expansion of canebrakes along edges and regeneration within gaps (West 1934, Marsh 1977, Gagnon & Platt 2008). However, the degree of density dependency and how regeneration is affected by it throughout a canebrake is unknown.

Density dependency may also explain an apparent tradeoff between regeneration and culm size observed in many bamboo species. For example, the leptomorphic bamboo *Sasa tsuboiana* Makino produces many small culms until reaching a density “full state” (density at which self-thinning begins to occur), at which point it produces fewer, but larger, culms (Makita 1996). In a non-bamboo clonal species, integration or connections between rhizomes has been shown to reduce density dependent responses. The number of new rhizomes and rosettes produced by unconnected rhizomes of *Solidago canadensis*

(L.), decreased as density increased, but interconnected ramets were not as sensitive to density (Hartnett & Bazzaz 1985). Because most canebrakes today are unable to expand beyond their current boundaries due to habitat loss, regeneration must occur within the canebrake where competition could limit production of new culms. However, whether density dependency is modified by integration among rhizomes is unknown in river cane.

River cane culm diameter and height vary greatly, from 3-25 mm and from a few centimeters to greater than 9 m, respectively (Hughes 1951, Marsh 1977). Gagnon et al. (2007) suggest that culms emerging within a canebrake are taller than surrounding culms due to competition with mature culms for light. Variation in culm diameter is due in part to rhizome size because culms are equal to or slightly greater than the diameter of the rhizome from which they emerge (West 1934, Marsh 1977). Rhizome diameter does not increase after initial growth, although new growth from the apex (tip) can continue unless the apex becomes a terminal culm (Marsh 1977). As in other bamboos, the rhizome system matures and nutrients build up in the rhizome so that new culms or rhizomes can be produced from lateral buds. The new rhizomes branch at acute angles in river cane and can be greater in diameter than the rhizome from which they branch (McClure 1966, Marsh 1977, Austin & Ueda 1978, Farrelly 1984, Liese 1998). The rhizomes continue to branch over successive seasons which causes them to mat and weave together forming a canebrake and increasing culm density (Marsh 1977). Therefore, older canebrakes should produce larger diameter culms, which is also typical of other bamboo species (West 1934, McClure 1966, Marsh 1977, Farrelly 1984).

In other bamboo species culm diameter and the total height are highly positively correlated (Austin & Ueda 1978). However, the relationship between culm height and diameter in river cane is unclear. Although Marsh (1977) observed no correlation between culm height and other morphological features in river cane, an increase in culm diameter as height increased was reported in the pachymorphic (clumping) bamboo *Chusquea culeou* Desvaux. Additionally, culm diameter in *B. fangiana* and *Fargesia robusta* Yi was greater where leaf biomass and culm height were greater (Taylor & Zisheng 1993, Pearson et al. 1994). In river cane, leaves are produced on lateral branches that emerge from buds at the nodes of the culms (McClure 1966, Marsh 1977, Farrelly 1984). Culms from younger rhizome systems have buds that produce branches along the entire length of the culm, while the lower nodes on culms arising from older rhizomes systems are often free of buds and thus are branch free for almost half the culm's total height (Marsh 1977). If morphological characteristics are correlated in river cane, and culm height is affected by competition for light, then density could also affect culm diameter and branch free height. However, the relationships between density and culm diameter, branch free height, and total height are unknown.

River cane is an important cultural resource for the Eastern Band of Cherokee Indians in western North Carolina. Cherokee artisans use river cane culms primarily for basket weaving, and there is a shortage of cane of sufficient quality for their work. They require culms with a branch free height of at least 2 m and a diameter of 15 mm and greater (David Cozzo personal communication, August 2008). In farming, crops are evenly dispersed to maximize yield in a confined space since density limits growth in many plants (Harper 1977). If the same holds true in river cane we may need to alter management practices to maintain regeneration of canebrakes, which are confined by human activities. If culm diameter, branch free height, and total height are influenced by density, as related characteristics are in forest ecology where higher densities cause trees to grow taller to compete for light, self-thin to reduce competition, and lose lower branches to dedicate more biomass to more effectively capture light, we may need to thin canebrakes (Harper 1977, Silvertown 1987). However, without knowing the patterns of density and where the higher quality culms occur simply thinning the entire brake may not be the best management practice. It is important to determine whether there is the same positive correlation in culm diameter and height as seen in other bamboos as these serve as indicators of canebrake health. If there is an optimum gap size that promotes regeneration of tall, large-diameter cane that is relatively free of branches, these gaps could be created through harvesting, and determining the patterns may indicate where best to harvest within a canebrake.

The purpose of this study was to improve our understanding of the relationships among canebrake density, regeneration, and young culm morphology in an effort to improve management of an important natural and cultural resource. I hypothesized that canebrake areas with greater culm density would have fewer young culms. Additionally, greater density would lead to smaller young culm diameters and shorter heights. I hypothesized that density was greater in the interior of a canebrake. The interior would also have young culms that would be larger in diameter and taller. Finally, I hypothesized that diameter, branch free height, and total height was positively correlated in young culms.

Materials & Methods

Sites and Sampling

Four mature canebrakes in western NC (Figure 1), large enough for at least 30 sample plots, were selected. A canebrake was considered mature if the majority of the culms had leafy tops beginning at heights above 2 meters, which is a criterion the Cherokee artisans use (David Cozzo personal communication, August 2008). The boundaries of each canebrake were defined based on the point where vegetation other than river cane such as multi flora rose (*Rosa multiflora* Thunb.), Chinese privet (*Ligustrum sinense* Lour.), grass (graminoid spp.), or Japanese honeysuckle (*Lonicera japonica* Thunb.) became denser than the cane, or where there were distinct edges created by mowing, roads, water, or a stream bank. Overstory species were noted within the river cane site database for two of the sample sites (Griffith & McDowell 2008). Within the boundary delineated for each canebrake, parallel transects 3 m apart were established perpendicular to the long axis of the brake. The first plot on the first transect was established 0.5 m into the brake so that it was completely within the delineated canebrake boundary. Plots 1 m x 1 m in size were established every 3 m and in a staggered pattern from transect to transect in order to have a sample size greater than 30 plots for statistical analyses (Figure 2). Plots were not established where trees and boulders occupied more than 25% of the plot. The locations of the first and last plots were measured with a GPS for the purpose of mapping all plot locations in each canebrake.

All mature culms within each 1 m^2 plot were categorized as young or old and counted to quantify density and describe patterns of regeneration across a canebrake. Young and old culms were distinguished from each other based on the presence of culm

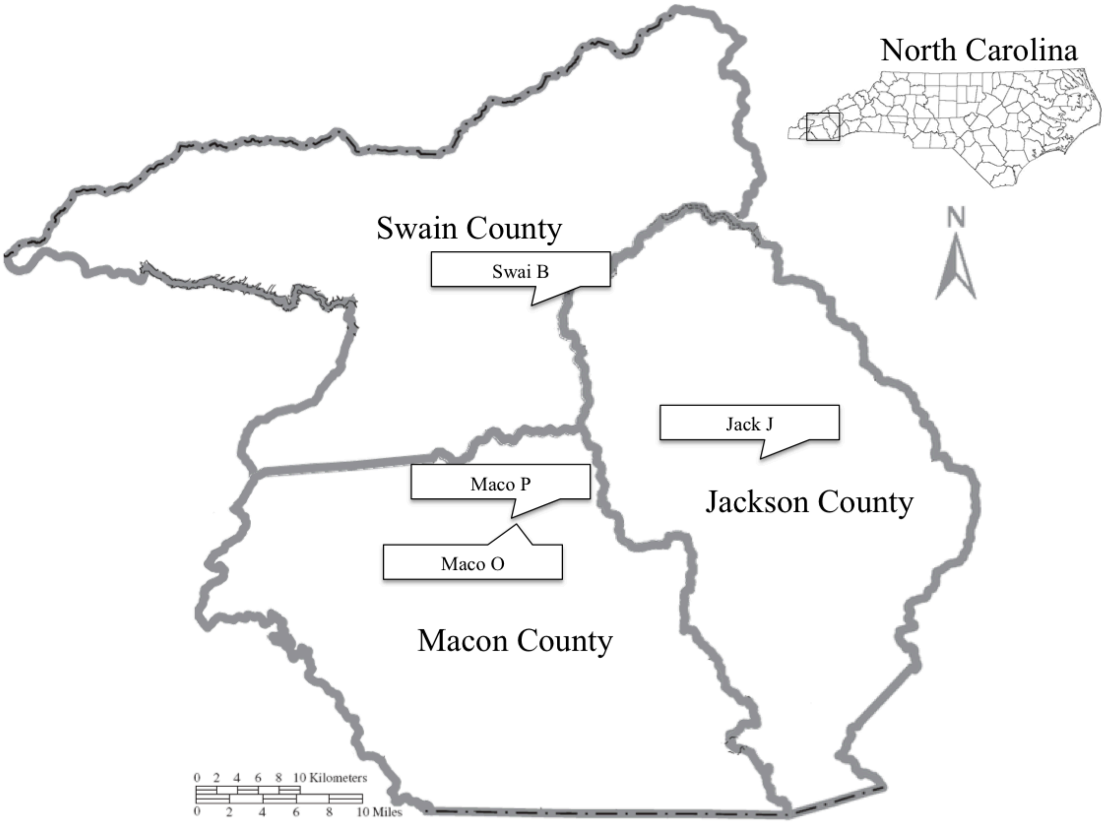


Figure 1. Locations of the four canebrake sites sampled in western North Carolina

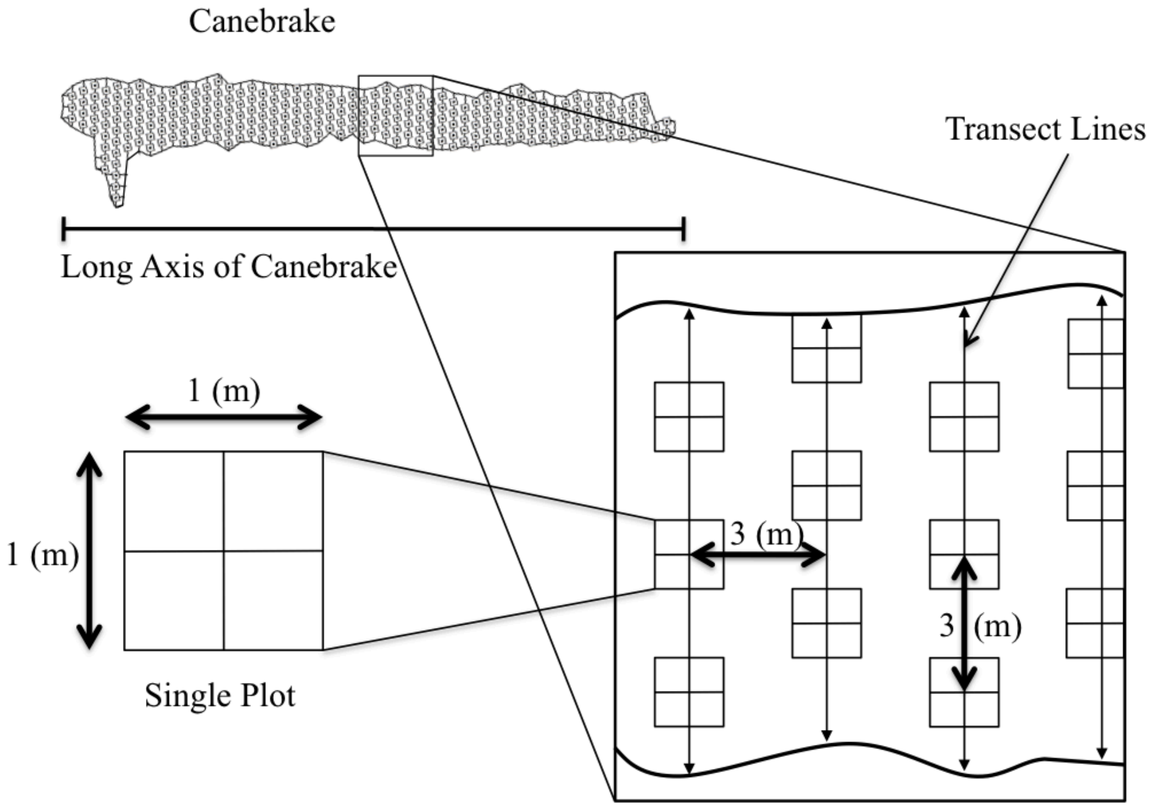


Figure 2. Sampling design and plot layout for river cane canebrakes in western North Carolina

sheaths. As culms get older, the sheaths covering the nodes dry, turn brown, and fall off (Marsh 1977). Culms categorized as young (1-3 years old) had at least one culm sheath and were used to represent the most recently regenerated of the mature culms. Mature culms categorized as old (3+ years old) had only sheath fragments (< 1/4 sheath left) or no sheaths. Each plot was divided into four quadrants for nearest neighbor analyses, which provide another way of estimating density (Pielou 1965). Nearest neighbor analysis used the distances between young culms and the nearest surrounding culm. In each quadrant that contained a mature young culm, the distance from the first young culm counted to the nearest old or young culm was measured to the nearest 0.5 cm.

Culm diameter, branch free height and total height were measured for all mature young culms to examine relationships between regenerating culm morphology and canebrake density. Culm diameter was measured with calipers 17 cm above the ground for standardization. Branch free height and total height were measured to the nearest cm using a height pole. Branch free height was measured from the ground to the first node that had a branch or a bud. When branching occurred at the ground the branch free height was recorded as zero. Total height was measured to the nearest cm from the ground to the top of the crown of the culm. Culms that were broken were counted for density and had diameter measured, but were not included in branch free or total height statistics.

Data Analysis

ArcInfo GIS (ESRI, 9.3) was used to map overall density, young culm density, and the morphology traits to provide a visual representation of the patterns in the variables measured. In particular, kriging was used to interpolate the patterns of density between plots generating an estimated surface. ArcInfo GIS was also used to determine whether density of young and old culms was randomly distributed or clumped using Moran's I index to help interpret possible relationships between density and regeneration patterns across a canebrake. Moran's I was also used to determine patterns in culm diameter, branch free height, and total height. Hot Spot Analysis in ArcInfo GIS was used to determine where there were high densities of young and old culm densities within each canebrake.

Linear regression using the R statistical program (R Foundation for Statistical Computing, 2.9.2, 2009) was used to test for relationships between young and old culm density, between overall density and morphology variables, between nearest neighbor distances and old culm density, and for relationships between culm diameters, branch free height, and total height. A critical p-value of 0.05 was used in all statistical tests. Where there were significant relationships but R^2 values were low, low density plots were deleted and the regression re-run in an effort to determine if there was a particular range of densities that explained a greater percent of the morphology and regeneration relationship.

Because linear relationships were weak, plots were placed into distance bands based on 3 m distance contours created in ArcInfo GIS. Analysis of variance (ANOVA) was used to determine if density and regeneration and the morphological variables differed among the distance classes. A critical p-value of 0.05 was used for all tests and where differences were significant, Tukey's mean separation was used to determine which distance classes differed from each other.

Results

General Site Description

The average area of the four canebrake sites was 1533.66 m^2 with the largest site (Maco O) 2550.29 m^2 and the smallest (Jack J) 1087.79 m^2 in size (Table 1). There were 624 total plots counted over the 4 sites with an average old culm density of 19.08 culms/m^2. A total of 948 young mature culms were measured within 346 plots that contained a young mature culm. All sites were within riparian zones, but only three had an edge right along a river. Associated overstory tree species vary between sites and include but are not limited to, red maple *(Acer rubrum* L.*),* dogwood *(Cornus florida* L.*),* black locust (*Robinia pseudoacacia* L.), black walnut (*Juglans nigra* L.), sycamore (*Platanus occidentalis* L.*)*, buckeye (*Aesculus Flava* Aiton) , and ironwood (*Carpinus caroliniana* Walter) (Griffith & McDowell 2008).

Regeneration

The density of young culms increased significantly ($p < 0.01$) as old culm density increased (Table 2). However, only 8% of the variation was explained by this relationship. When low density plots were deleted the percentage of variation explained did not improve. So while significant, the relationship is extremely weak across all densities of culms measured in the study. The distance between a young culm and its nearest neighbor decreased at higher old culm densities ($p <0.01$) but the amount of variation explained was 14% (Figure 3, Table 2).

Differences in density between distance from the edge classes were not significant for young or old culms ($p = 0.14$ and $p = 0.24$, respectively) (Figure 4, Table 3). Density of young and old culms did not change linearly from edge to interior (Figure 5). Old and

Table 1. Canebrake size and young culm characteristics in four canebrakes in western NC.

	Canebrake Size				Young Culms		
Site	Area (m^2)	Perimeter (m)	Total Plots	AVG Density ($\#/m^2$)	Culm Diameter (mm)	Branch Free Height (cm)	Total Height (m)
Maco P	1114.75	234.68	105	17.32	5.98	32.00	1.51
Maco O	2550.29	393.45	259	14.14	6.59	42.97	1.65
Swai B	1381.80	245.47	139	24.19	6.17	35.35	1.43
Jack J	1087.79	279.30	121	20.67	8.46	54.25	2.02
Average	1533.66	288.22		19.08	6.80	41.14	1.65
Total	6134.63		624				

Table 2. Relationships between young and old culm density as well as nearest neighbor distance and old culm density for canebrake sites in western NC

Relationship	Equation	Adjusted R^2	P Value
Young Culm Density ($\#/m^2$) vs. Old Culm Density ($\#/m^2$)	$y=0.06x+0.44$	0.08	<0.01
Nearest Neighbor (cm) vs. Old Culm Density ($\#/m^2$)	$y=-0.25+14.17$	0.14	<0.01

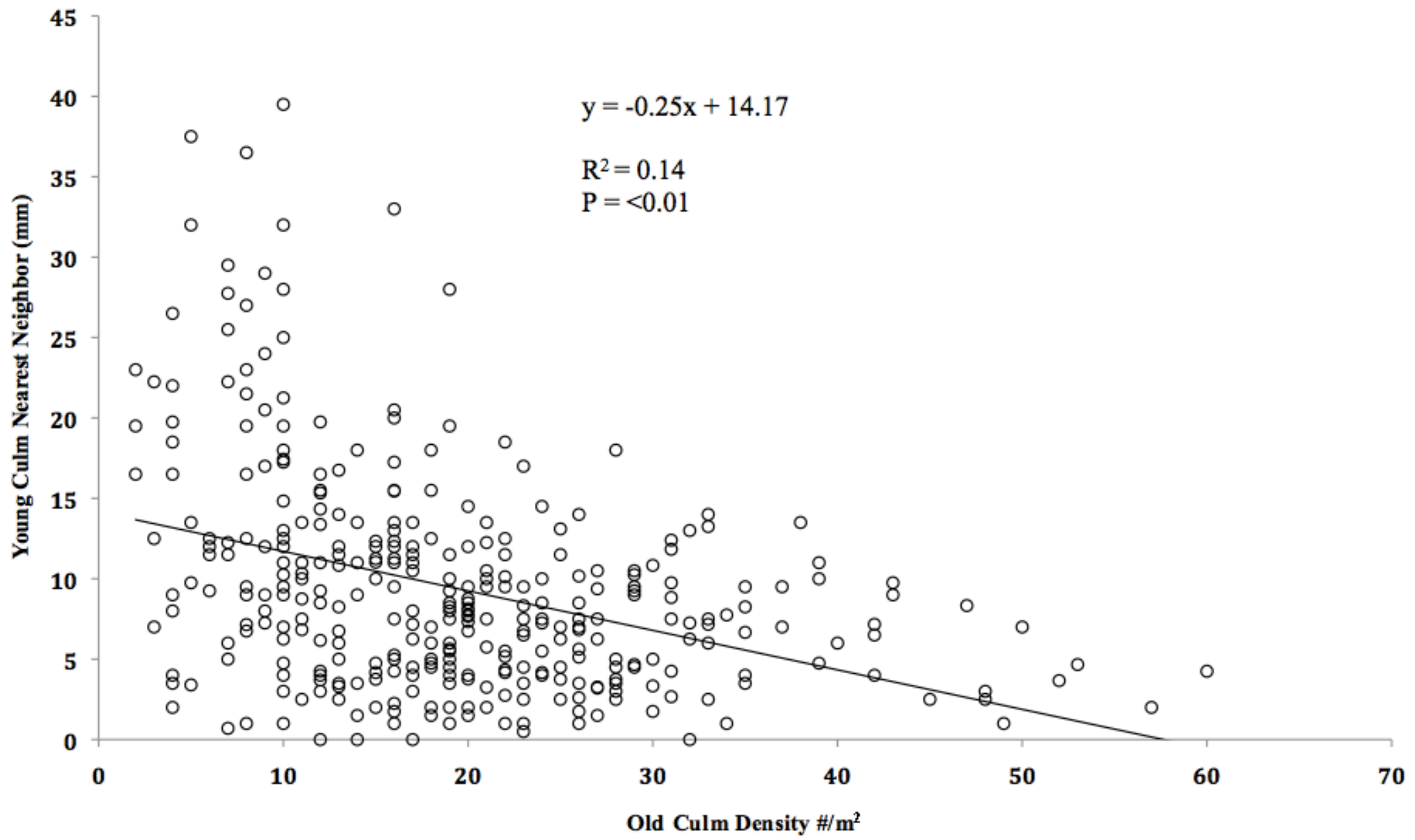


Figure 3. Relationship between nearest neighbor distance and old density for canebrake sites in western NC

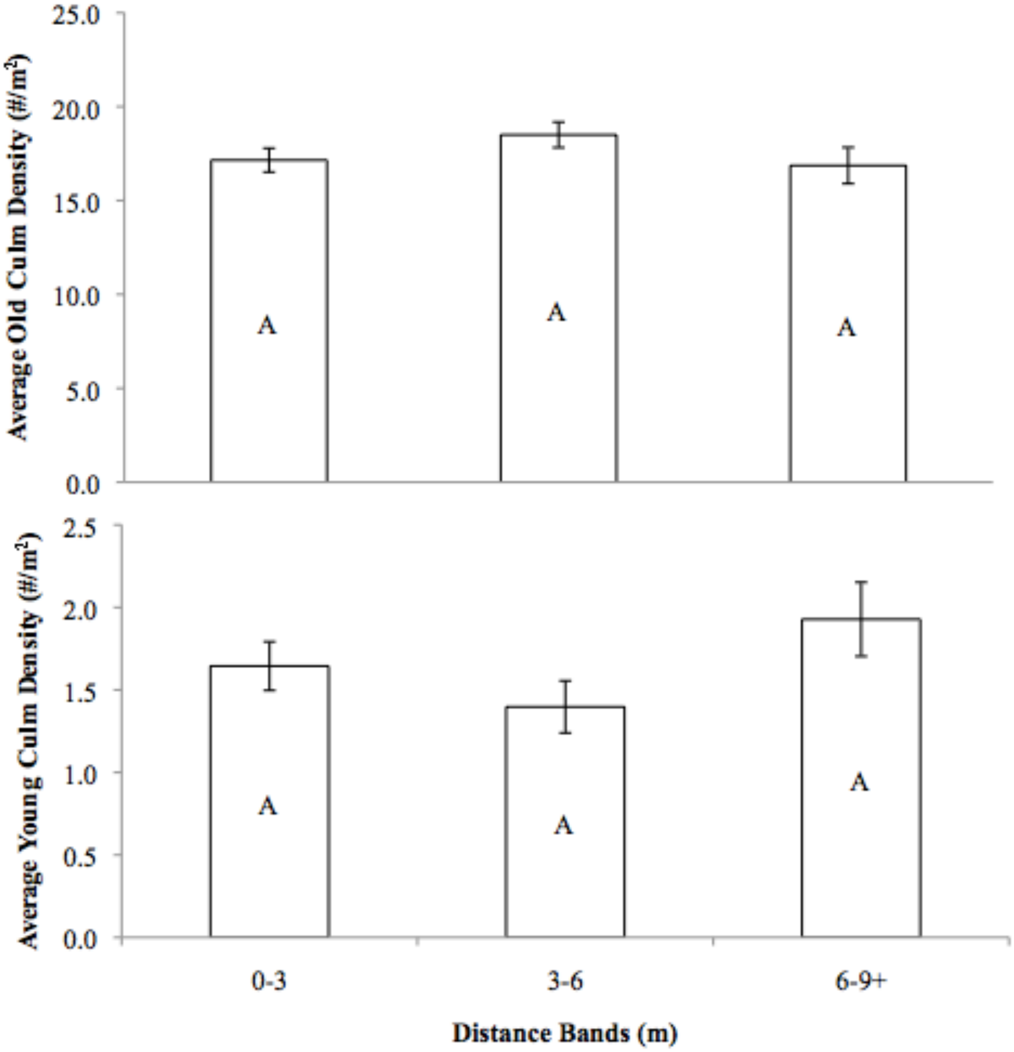


Figure 4. Differences between distance bands for average old and young culm densities with means separation for canebrake sites in western NC

Table 3. Differences among distance bands in old and young culm density and young culm morphological characteristics for canebrake sites in western NC

Variable	P Value
Young Culm Density (#/m^2)	0.14
Old Culm Density (#/m^2)	0.24
Average Culm Diameter (mm)	<0.01
Average Branch Free Height (cm)	<0.01
Average Total Height (m)	<0.01

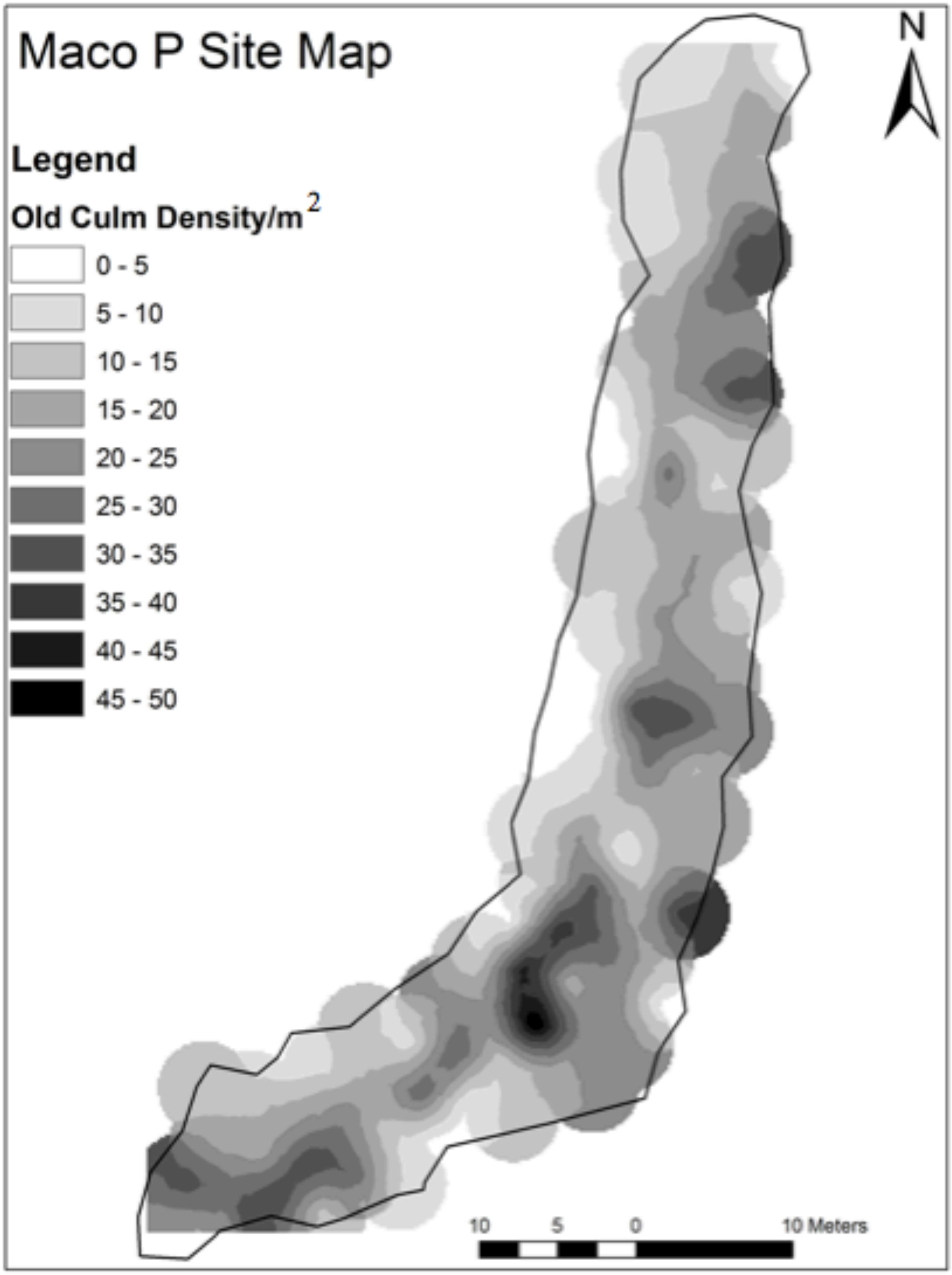


Figure 5. Example of density variability across a canebrake site using kriging interpolation to estimate a surface of density in Arc GIS

young culms were clustered in 3 out of 4 sites, with old culms randomly distributed only at Maco P and young culms randomly distributed only at Maco O (Table 4). Figure 6 illustrates hot spots of clusters of young and old culm density in each site indicating clusters of high and low values for density.

Morphology

The largest culms between the four canebrake sites were found in 114 plots with young mature culms where average young culm diameters were 15 mm or greater. The average old culm density of the 114 plots was 17.98/m^2. The average number of young culms for theses plots was 1.79/m^2. Relationships among culm diameter, branch free, and total height were all statistically significant ($p < 0.01$) (Figure 7). As culm diameter increased branch free and total height also increased ($R^2 = 0.62$ and 0.84 respectively). As the culms grew taller the branch free height also increased ($R^2 = 0.65$). Relationships between average culm diameter, branch free height, total height, and young culm density were significant ($p < 0.01$) (Table 5) but poor, with culm size tending to decrease as young culm density increased. The best relationships occurred when young culm densities less than 8 young culms/m^2 were deleted from the regression analysis. At 8 young culms/m^2 the relationship to young culm density for young culm diameter ($R^2 = 0.35$)(Figure 8), branch free height ($R^2 = 0.31$), and total height ($R^2 = 0.40$) all decreased as young culm density increased. Young culm diameter, branch free height, and total height relationships to old culm density was also significant with culm diameter ($p = 0.03$) and total height ($p = 0.01$) but not for branch free height ($p =0.24$) (Table 5). Culm diameter and total height tended to be smaller at higher old culm densities but only 2% of the variation was explained by these linear relationships. Differences among distance

Table 4. Results of Moran’s I Index analysis for each site by old and young culm densities for canebrake sites in western NC

Site	Stage	Moran's I	Z Score	Spatial Auto Correlation
Maco O	Old	0.21	3.04	Clustered
	Young	-0.05	-0.74	Random
Maco P	Old	0.06	0.64	Random
	Young	0.45	4.06	Clustered
Swai B	Old	0.25	3.46	Clustered
	Young	0.27	3.76	Clustered
Jack J	Old	0.45	4.88	Clustered
	Young	0.29	3.13	Clustered

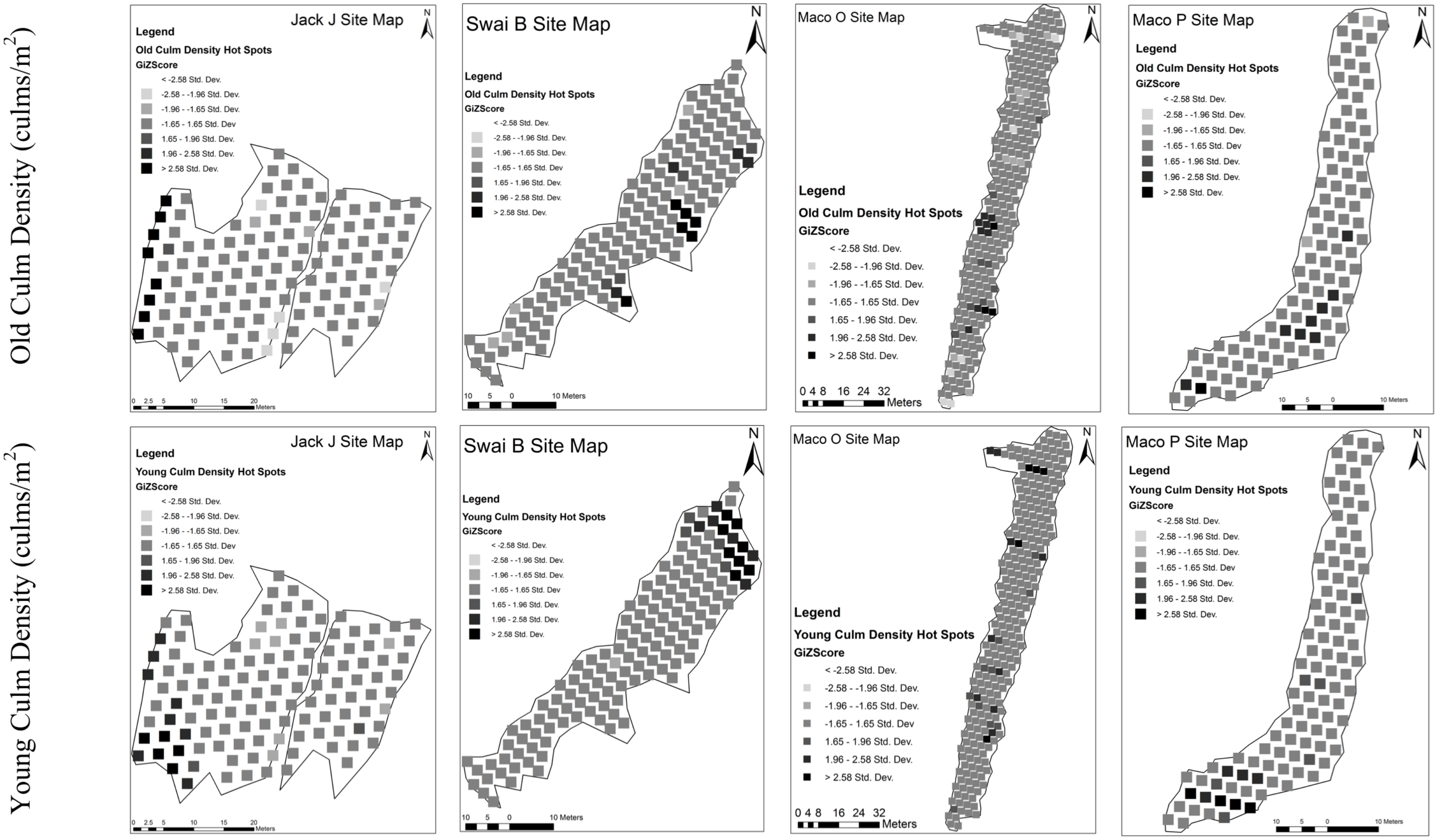


Figure 6. Hot spot analysis for old and young culm densities in all four canebrakes. Darker squares represent areas of high density clustering

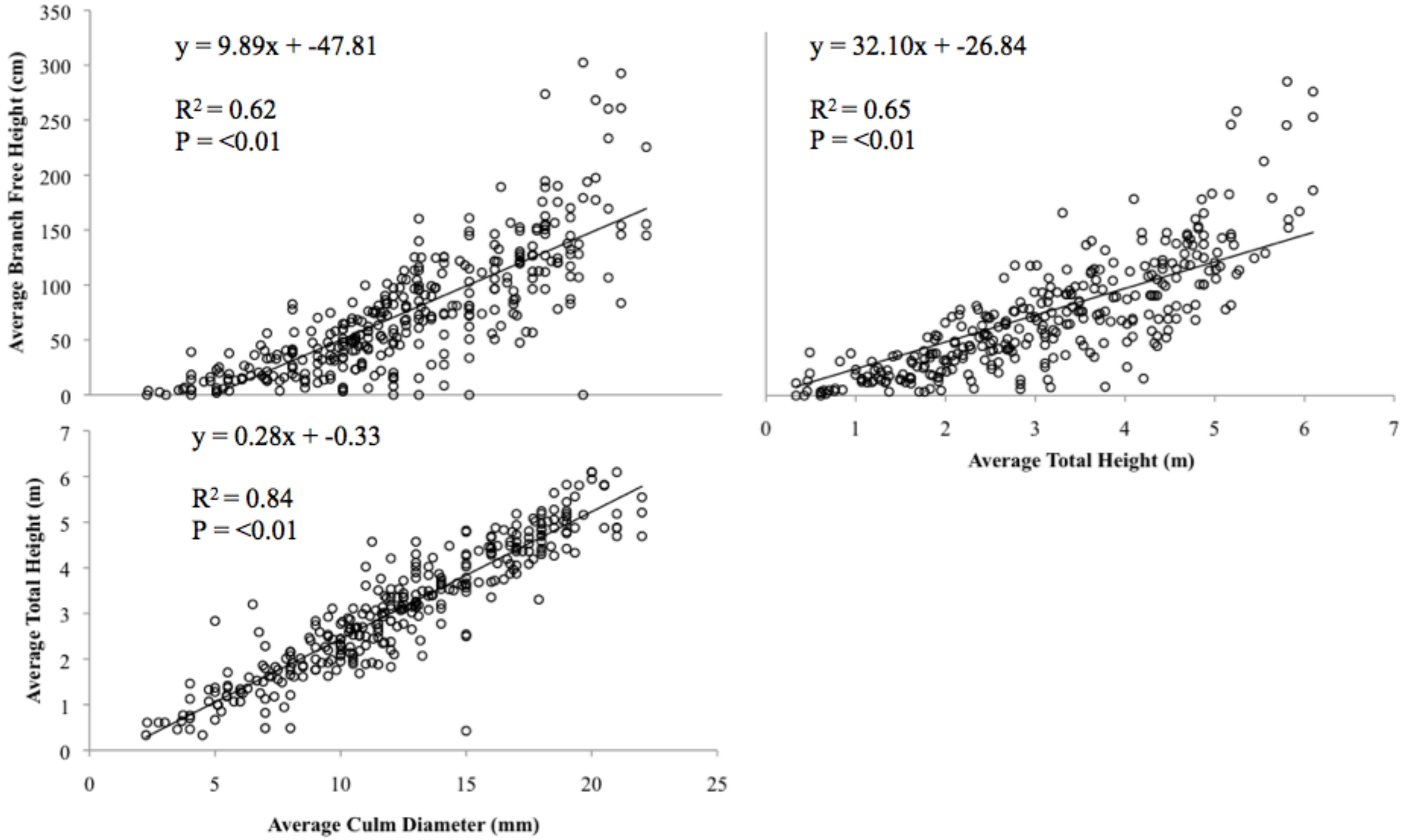


Figure 7. Linear regressions results for relationships morphological characteristics for canebrake sites in western NC

Table 5. Young and old culm density in relation to young culm morphologies for river cane canebrakes in western NC

	Young Culm Density		Old Culm Density	
Young Culm Morphology	Adjusted R^2	p Value	Adjusted R^2	p Value
Average Culm diameter (mm)	0.35	<0.01	0.010	0.03
Average Branch Free Height (cm)	0.31	<0.01	0.001	0.24
Average Total Height (m)	0.40	<0.01	0.020	0.01

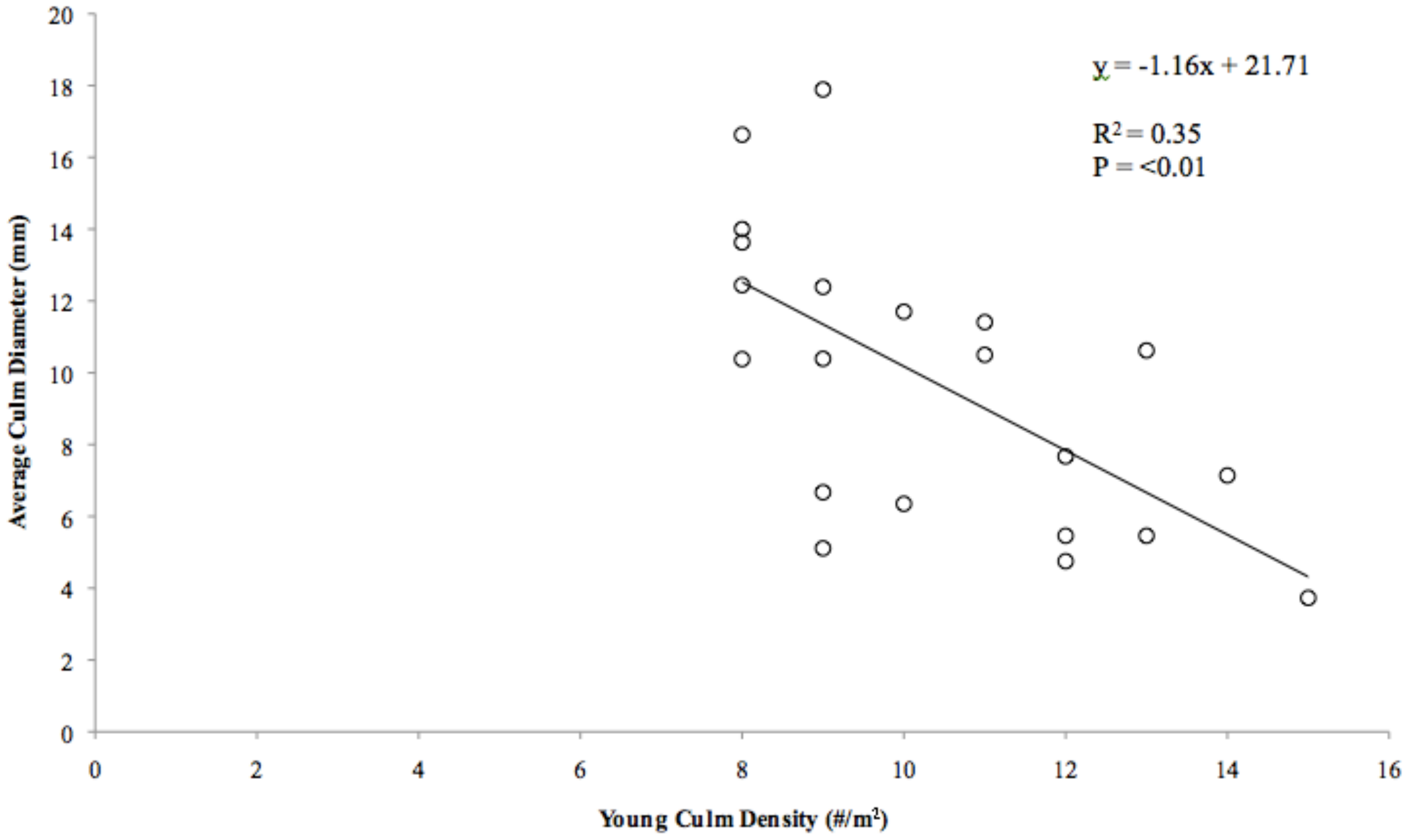


Figure 8. Relationship between culm morphology and regeneration for canebrake sites in western NC

from the edge classes were statistically significant for morphology variables ($p < 0.01$) (Table 3). Culms had significantly greater branch free height, were taller, and had larger diameters 3 meters or more into the interior (Figure 9). Culm morphology spatial autocorrelation was variable across the four sites (Table 6). In Maco O and Jack J the culm morphologies were randomly distributed. In Maco P the culm morphologies were clustered, but culm diameter and branch free height were dispersed in Swai B while total height was random.

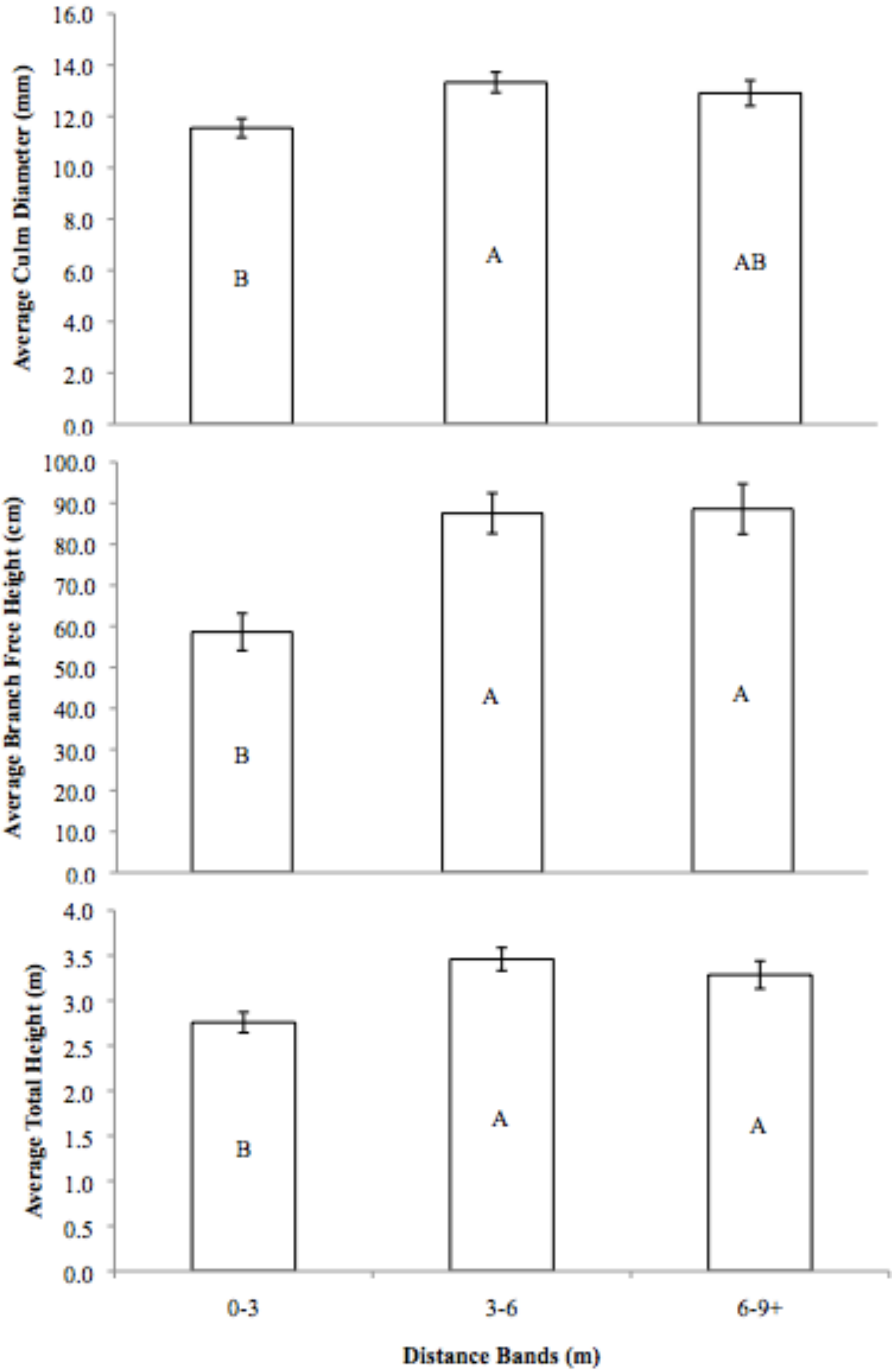


Figure 9. Culm morphology differences amongst 3 (m) distance bands with means separation in western NC

Table 6. Results of Moran’s I Index analysis for each site and corresponding culm morphological characteristics for canebrake sites in western NC

Spatial Auto Correlation	Culm Diameter		Branch Free Height		Total Height	
Site	Moran’s I	Z-Score	Moran’s I	Z-Score	Moran’s I	Z-score
Maco O	Random		Random		Random	
	-0.01	-0.13	0.06	0.99	-0.01	-0.13
Maco P	Clustered		Clustered		Clustered	
	0.39	3.55	0.24	2.19	0.40	3.57
Swai B	Dispersed		Dispersed		Random	
	-0.17	-2.19	-0.16	-2.14	-0.07	-0.92
Jack J	Random		Random		Random	
	0.12	1.31	-0.05	-0.39	0.14	1.54

Discussion

My hypothesis that old culm density was related to regeneration was supported, although the relationship was very weak and opposite in direction to what I expected. Taylor & Zisheng (1993) found less regeneration in areas of higher densities in a leptomorphic bamboo. This is the relationship I expected to find and my results could have differed if the canebrakes I sampled had not reached a density full state so regeneration was still high (Makita 1996). However, the average density in all four sites only varied by 10 culms/m^2 indicating the regeneration may be maintaining a specific density (Hutchings 1979) and suggesting the canebrakes I sampled had reached a density full state. The relationship between nearest neighbor distance and old culm density was also significant but weak. Distances between regenerating culms and their nearest neighbor even reached zero for a few of the plots. This suggests that the density full state for river cane is high with culms having high survivability (self-tolerance) despite being so near to each other. However, tillering which is the growth of a culm from the base of another culm, may account for some the lowest distance values but was not reported to be a common occurrence in river cane canebrakes (Hughes 1951, Marsh 1966).

The poor relationship between regeneration and density could be due to clonal integration, modifying expected density-dependent regeneration responses (Harper 1977, Hutchings 1979, DeKroon & Kwant 1992). This has been reported in dwarf bamboo *Sasa palmata* (Marlic) Nakai where greater culm density occurred among connected rhizomes (Saitoh et al. 2002). In addition to clonal integration modifying expected density-dependent regeneration, it could explain why densities of regeneration were not higher closer to the edge of canebrakes where competition for resources would be expected to be lower thus supporting greater number of young culms. In the sampled river cane canebrakes, young and old culm densities were heterogeneous throughout the canebrakes. Clusters of higher densities may reflect areas of greater resources that support greater culm production with competition between culms likely mediated by clonal integration (Harper 1977). In the site where young culm density was randomly distributed, it is possible that the long and narrow shape could account for this result. In the site with random old culm distribution the result was likely due to the small size of the canebrake. Resources such as light, water, and nutrients often have patchy distributions (Roberston & Gross 1994, Jackson & Caldwell 1996, Hutchings et al. 2003). Therefore, the occurrence of high-density patches of river cane could simply be related to patchiness of resources (Salzman 1985, McNickle & Cahill 2009).

In the bamboo *Phyllostachys pubescens* (Mazel) Ohwi, survival of new shoots decreased with increasing distance from already established shoots, indicating that older shoots may provide resources for new shoots (Li et al. 1998 c). Noguchi and Yoshida (2005) reported clonal integration could support persistence of the dwarf bamboos *Sasa kurilensis* (Ruprecht) and *Sasa senanensis* (Franchet et Savatier) in resource poor locations. Because there is little variation in soil nutrients across a canebrake (Griffith 2008), and river cane can survive in a variety of soil types and drainage conditions (West 1934, Marsh 1977, Cirtain 2004, Griffith 2008, Cirtain et al. 2009), light may be an important limiting resource. Light is often a limiting resource for grasses (Kozlowski et al. 1997) and river cane seedling germination has been found to be dependent on light (Baldwin et al. 2009, Cirtain et al 2009). New vegetatively reproduced culms compete with surrounding established culms for light (Gagnon et al. 2007) further supporting that the patchiness of river cane densities could be light dependent rather than below ground resource dependent. The canebrakes I studied occurred in association with different tree species that produce different understory microhabitats including heterogeneous light (Corzier & Boerner 1984, Clinton 2003, Cirtain et al 2009). Other studies have shown that greater light results in greater river cane regeneration (Gagnon et al. 2007, Cirtain et al. 2009, Osland et al. 2009).

The strong relationships between culm diameter, branch free height, and total height found in this study are similar to results in other bamboos (Marsh 1977, Taylor & Zisheng 1993, Pearson et al. 1994). River cane culms were taller, had greater branch free height, and greater culm diameters within the canebrake interior. However, these characteristics were randomly distributed in two sites while in one site the characteristics were clustered and another they were dispersed. The variation in distribution may be due to size and shape of the canebrake, as the clusters were found in the smallest canebrake that also had the fewest plots with young culms. It may also be that overstory trees are leading to the random pattern in the two largest canebrakes and the canebrake with dispersed distribution had less of an overstory.

Culm diameter is equal to or slightly larger than the rhizome diameter and older rhizomes support new rhizomes that may be larger in diameter (West 1934, McClure 1966, Marsh 1977). This means that new culms that emerge from nodes of new rhizomes branching from older rhizomes within a canebrake would be expected to have larger diameters and be taller because they are competing with surrounding mature culms for light (West 1934, McClure 1966, Marsh 1977, Gagnon et al. 2007). Finally, it is possible that the hot spots and clustering represent areas of original colonizations. Multiple dense smaller canebrakes could have expanded to form a single large canebrake when the multiple colonies merged to become the current canebrake (Gagnon et al. 2007).

My results indicating areas of greater regeneration produced culms that tended to be smaller in size is consistent with studies showing smaller sized regenerating culms in gaps and away from the edge of the canebrake where rhizomes are spreading (Marsh 1977, Gagnon et al. 2007). This resource allocation tradeoff between regeneration amount and size of regenerating culms has been reported to occur during the transition from populating an open area to when that area has reached a density full state (Hartnett & Bazzaz 1983, Makita 1996, Yue et al. 2004, Cirtain et al. 2009). Resource allocation tradeoffs have been reported in several other bamboo species especially related to light and environmental heterogeneity. In the bamboo *Phyllostachys praecox* f. *prevernalis*, increasing light led to greater number of new shoots while decreasing light due to overstory canopy shading resulted in greater aerial biomass allocation. Clonal morphology has been reported to shift from clumping to spreading depending on light availability (Yue et al. 2004). In the bamboo *Fargesia nitida* (Mitford) Keng f. et Yi, resources were allocated to enlarging leaves, rhizomes, and root mass to support greater lateral growth at the expense of culm mass in unfavorable understory light conditions (Yu et al. 2006). These trade-offs could explain the negative relationship between regeneration and culm diameter, branch free height and total height.

Clonal integration can also contribute to the lack of relationship between density and morphology. For example, clonal integration in the dwarf bamboo *S. palmata* resulted in increased mass when shaded ramets and ramets receiving full sun were connected compared to when the rhizomes were severed (Saitoh et al. 2002). Even though young culms were competing more for light at higher densities, integration with greater numbers of old culms could support the new culms. In the leptomorphic giant bamboo (*Phyllostachys pubescens* (Mazel) Ohwi), increased survival of new shoots, particularly those closer to a parent culm were attributed to translocation of resources (McClure 1966, Li et al. 1998 a & b). The translocated resources affecting both regeneration and morphology may be carbohydrates, which are needed for growth of new structures and are stored in the rhizomes (Li et al. 1998c, Brendecke 2008, Zaczeck et al. 2009b). It is worth noting that the most effective way of propagating a canebrake is by removing clumps of whole cane with the rhizomes intact and transplanting them (Dattilo & Rhoades 2005, Baldwin et al. 2009). This maintains the clonal integration for the clump and so long as one or two culms survive they can possibly support new growth.

In conclusion, my results suggest that river cane is able to take advantage of resource patches and regenerate within the canebrake to the point where it probably reaches a density full state. Culms produced at density full states are larger and could support further spread of the canebrake. Therefore, creating “gaps” by thinning out smaller culms is probably more effective to promote regeneration of larger sized culms than uniform thinning. As noted in the results, the average density for plots containing the largest cane was $17.98/m^2$. This might be a starting density to thin “gaps” within canebrakes. Additionally, light appears to be an important factor so thinning overstory tree canopies in combination with thinned “gaps” may further increase culm diameters of regenerating culms (Cirtain et al. 2009).

The degree to which clonal integration regulates density and regeneration needs further study and, when combined with specific resource information, may suggest a spatial pattern for optimum thinned “gap” creation. Creating thinned “gaps” within canebrake interiors, where the larger rhizomes are located could increase regeneration of culms that are of the quality needed for Cherokee artisans. Creating thinned “gaps”, as opposed to creating a complete opening would leave some culms for new culms to compete with for light thus stimulating height growth. Management practices that allow canebrake perimeters to expand should also promote an increase in the quantity and quality of cane over time by increasing total interior area and allowing older rhizomes to support larger new rhizome growth over time. There is need for further study of the relationships between regeneration and culm diameter, branch free height and total height to determine the optimal density to promote regeneration and create optimal culm characteristics.

CHAPTER 4: LITERATURE CITED

Alpert P. 1991. Nitrogen sharing among ramets increases clonal growth in *Fragaria chiloensis*. Ecology 72:69-80

Alpert P. 1999. Effects of clonal integration on plant plasticity in *Fragaria chiloensis*. Plant Ecology 141:96-106

Alpert P and Mooney HA. 1986. Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. Oecologia 70:227-233

Austin R and Ueda K. 1978. Bamboo. New York and Tokyo. Weatherhill Inc.

Baldwin BS, Cirtain M, Horton DS, Ouellette J, Franklin SB, and Preece JE. 2009. Propogation methods for river cane [*Arundinaria gigantea* L. (Walter) Muhl.]. Castanea 74:300-316

Blattel CR, Williard KWJ, Baer SG, and Zackzek JJ. 2005. Abatement of ground water phosphate in giant cane and forest riparian buffers. Journal of the American Water Resources Association 41:301-307

Brantley CG and Platt SG. 2001. Canebrake conservation in the southeastern United States. Wildlife Society Bulletin 29:1175-1181

Brendecke WW. 2008. The effect of collection and establishment season, planting orientation and attached culms on the survival and growth of *Arundinaria gigantea* (Walt.) Muhl. (Giant Cane) rhizome propagules. Master of Science Thesis. Southern Illinois University Carbondale. 67 p.

Briske DD and Butler JL. 1989. Density-dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium* interclonal versus intraclonal interference. Journal of Ecology 77:963-974

Cirtain M. 2004. Effects of nitrogen and moisture regimes on *Arundinaria gigantea* (Walt.) Muhl. seedling growth. Natural Areas Journal 24:251-257

Cirtain MC, Franklin SB, and Pezeshki R. 2009. Effect of light intensity on *Arundinaria gigantea* growth and physiology. Castanea 74:236-246

Clinton BD. 2003. Light, temperature, and soil moisture responses to elevation, evergreen, understory, and small canopy gaps in the southern Appalachians. Forest Ecology and Management 186:243-255

Crozier CR and Boerner EJ. 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. Oecologia 62:337-343

Dattilo AJ and Rhoades CC. 2005. Establishment of woody grass *Arundinaria gigantea* for riparian restoration. Restoration Ecology 13:616-622

DeKroon H and Kwant R. 1991. Desnity-dependent growth responses in two clonal herbs: Regulation of shoot density? Oecologia 86:298-304

DeKroon H, Hara T, and Kwant R. 1992. Size hierarchies of shoots and clones in clonal herb monocultures: Do clonal and non-clona plants compete differently. Oikos 63:410-419

DeKroon H and Hutchings MJ. 1995. Morphological plasticity in clonal plants: The foraging concept reconsidered. Journal of Ecology 83:143-15

Evans JP. 1992. The effect of local resource availability and clonal integration on ramet functional morphology in *Hydrocotyle bonariensis*. Oecologia 89:265-276

Farrelly D. 1984. The book of bamboo. San Francisco. Sierra Club Books. 332p

Gagnon PR, Platt WJ, and Moser EB. 2007. Response of a native bamboo [*Arundinaria gigantea* (Walt.) Muhl.] in a wind-disturbed forest. Forest Ecology and Management 241:288-294

Gagnon PR and Platt WJ. 2008. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. Ecology 89:612-618

Griffith A, McDowell K, and Young R. 2007. River cane sites in western North Carolina: A revitalization of traditional Cherokee artisan resources initiative. 2nd Ed. Unpublished Report, Center for Coastal Studies, Western Carolina University, Cullowhee, NC

Griffith AD, Kinner DA, Tanner BR, Moore A, Mathews KG, and Young RS. 2009. Nutrient and physical soil characteristics of river cane stands, western North Carolina. Castanea 74:224-235

Harper JL. 1977. Population biology of plants. New York: Academic Press. 892p

Hartnett DC and Bazzaz FA 1983. Physiological integration among intralclonal ramets in *Solidago canadensis*. Ecology 64:779-788

Hartnett DC and Bazzaz FA. 1985. The regulation of leaf, ramet, and genet densities in experimental populations of the rhizomatous perennial *Solidago canadensis*. Journal of Ecology 73:429-443

Hill SH. 1996. Weaving history: Cherokee baskets from the Springplace mission. The William and Mary Quarterly 53:115-136

Hughes RH. 1951. Observations of cane (*Arundinaria*) flowers, seed, and seedlings in the North Carolina coastal plain. Bulletin of the Torrey Botanical Club 78:113-121

Hunter WC, Buehler DA, Canterbury RA, Confer JL, and Hamel PB. 2001. Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29:44-455

Hutchings MJ. 1979. Weight-density relationship in ramet populations of clonal perennial herbs, with special reference to the -3/2 power law. Journal of Ecology 67:21-33

Hutchings MJ, John EA, and Wijesinghe DK. 2003. Toward understanding the consequence of soil heterogeneity for plant populations and communities. Ecology 84:2322-2334

Jackson RB and Caldwell MM. 1993. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74:612-614

Jackson RB and Caldwell MM. 1996. Integrating resource heterogeneity and plant plasticity: modeling nitrate and phosphate uptake in a patchy soil environment. Journal of Ecology 84:891-903

Kozlowski TT, Pallardy SG, and Kramer PJ. 1997. Physiology of woody plants. San Diego: Academic Press 411p

Li R, During HJ, Werger MJA, and Zhong ZC. 1998a. Positioning of new shoots relative to adult shoots in groves of giant bamboo, *Phyllostachys pubescens*. Flora 193:315-321

Li R, Werger MJA, During HJ, and Zhong ZC. 1998b. Biennial variation in production of new shoots in groves of the giant bamboo *Phyllostachys pubescens* in Sichuan, China. Plant Ecology 135:103-112

Li R, Werger MJA, During HJ, and Zhong ZC. 1998c. Carbon and nutrient dynamics in relation to growth rhythm in the giant bamboo *Phyllostachys pubescens*. Plant and Soil 201:113-123

Liese W.1998. The anatomy of bamboo culms. Beijing:International network for bamboo and rattan. Technical report 18 208p

Lyon J and Gross NM. 2005. Patterns of plant diversity and plant-environmental relationships across three riparian corridors. Forest Ecology and Management 204:267-278

Makita A. 1996. Density regulation during the regeneration of two monocarpic bamboos: self-thinning or intraclonal regulation. Journal of Vegetation Science 7:281-288

Makita A. 1998. The significance of the mode of clonal growth in the life history of bamboos. Plant Species Biology 13:85-92

Marsh DL. 1977. The taxonomy and ecology of cane, *Arundinaria gigantea* (Walter) Muhlenburg. Ph.D. Dissertation. University of Arkansas. Little Rock, AR. 302 p.

Mathews KG, Hughuelet J, Lanning M, Wilson T, and Young RS. 2009. Clonal diversity of *Arundinaria gigantea* (Poaceae; Bambsoideae) in western North Carolina and its relationship to sexual reproduction: an assessment using AFLP fingerprints. Castanea 74:213-223

McClure FA. 1966. The bamboos: a fresh perspective. Cambridge: Harvard University Press 347p

McNickle GG and Cahill JF Jr. 2009. Plant root growth and the marginal value theorem. Proceedings of the National Academy of Science 106:4747-4751

Meanley B. 1972. Canebrakes of the Ocmulgee. Pages 46-48 in: Swamps, river bottoms and canebrakes. Barre: Barre Publishing. 142p

Neal DM, Jolley R, Baldwin B, Ervin G, Certain M, Seymour J, and Campbell J. 2010. Maximizing seed germination methods to enhance Rivercane [*Arundinaria gigantea* L. (Walter) Muhl] seedling production for habitat restoration programs. Unpublished Presentation at Association of Southeastern biologists.

Noguchi M and Yoshida T. 2005. Factors influencing the distribution of two co-occurring dwarf bamboo species (*Sasa kurilensis* and *S. senanensis*) in a conifer-broadleaved mixed stand in northern Hokkaido. Ecological Restoration 20:25-30

Noss RE, Laroe III ET, and Scott JM. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. United States Department of Interior, National Biological Service, Biological Report 28, Washington D.C., USA.

Osland MJ, Pahl JW, and Richardson CJ. 2009. Native Bamboo [*Arundinaria gigantea* (Walter) Muhl., Poaceae] Establishment and growth after the removal of an invasive non-native shrub (*Ligustrum sinense* Lour., Oleaceae): Implications for restoration. Castanea 74:247-258

Pearson AK, Pearson OP, and Gomez IA. 1994. Biology of the bamboo *Chusquea culeou* (Poaceae: Bambusoideae) in southern Argentina. Vegetatio 111:93-126

Pielou EC. 1959. The use of point-to-plant distances in the study of the pattern of plant populations. Journal of Ecology 47:607-613

Platt SG and Brantley CG. 1997. Canebrakes: An ecological and historical perspective. Castanea 62:8-21

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reid DG, Taylor AH, Jinchu H, and Zisheng Q. 1991. Environmental influences on bamboo *Bashania fangiana* growth and implications for giant panda conservation. Journal of Applied Ecology 28:855-868

Roberston PG, Hutson MA, Evans FC, and Tiedje JM. 1988. Spatial variability in a successional plant community: Patterns of nitrogen availability. Ecology 69:1517-1524

Robertson GP and Gross KL. 1994. Assessing the heterogeneity of belowground resources: quantifying pattern and scale. Pages 237-253 in: Exploitation of environmental heterogeneity by plants. Academic Press Inc. 429p

Saitoh T, Seiwa K, and Nishiwaki A. 2002. Importance of physiological integration of dwarf bamboo to persistence in forest understory: A field experiment. Journal of Ecology 90:78-85

Salzman AG. 1985. Habitat selection in a clonal plant. Science 228:603-604

Schoonover JE, Willard KWJ, Zaczek JJ, Mangun JC, and Carver AD. 2005. Nutrient attenuation in agricultural surface runoff by riparian buffer zones in southern Illinois, USA. Agroforestry Systems 64:169-180

Schoonover JE, Willard KWJ, Zaczek JJ, Mangun JC, and Carver AD, 2006. Agricultural sediment reduction by giant cane and forest riparian buffers. Water Air and Soil Pollution 169:303-315

Sharpe GW, Hendee JC, and Shape WF. 2003. Watersheds and streams. Pages 230-232 In Introduction to forests and renewable resources. NY: McGraw-Hill Inc.

Shepherd WO. 1952. Highlights of forest grazing research in the southeast. Journal of Forestry 280-283

Silvertown JW. 1987. Introduction to plant population ecology: 2nd ed. Longman Scientific & Technical co-published with John Wiley & Sons, Inc NY. 229p

Slade AJ and Hutchings MJ. 1987a. The effects of nutrient availability on foraging in the clonal herb *Glechoma hederacea*. Journal of Ecology 75:95-112

Slade AJ and Hutchings MJ. 1987d. An analysis of the costs and benefits of physiological integration between ramets in the clonal perennial herb *Glechoma hederacea*. Oecologia 73:425-431

Taylor AH and Zisheng Q. 1993. Structure and dynamics of bamboos in the Wolong natural reserve, China. American Journal of Botany 80:375-384

Triplett JK, Weakley AS, and Clark LG. 2006. Hill cane (*Arundinaria appalachiana*), A new species of bamboo (Poaceae:Bambusoideae) from the southern Appalachian mountains. SIDA 22:79-95

Triplett JK and Clark LG. 2010. Phylogeny of the temperate bamboos (Poaceae: bambusoidaea; bambuseae) with an emphasis on *Arundinaria* and allies. Systematic Botany 35:102-120

Vanclay KJ and Sands PJ. 2009. Calibrating the self-thinning frontier. Forest Ecology and Management 259:81-85

West E. M. 1934. Canebrakes of the southeastern United States. PhD. Dissertation. The Ohio State University, Columbus, Ohio.

White J and Harper JL. 1970. Correlated changes in plant size and number in plant populations. Journal of Ecology 58:467-485

Wijesinghe DK and Handel SN. 1994. Advantages of clonal growth in heterogeneous habitats: and experiment with *Potentilla simplex*. Journal of Ecology 82:495-502

Yu X, Tao J, Li Y, Wang Y, Xi Y, Zhang W, and Zang R. 2006. Ramet population structure of *Fargesia nitida* (Mitford) Keng f. et Yi in different successional stands of the subalpine coniferous forest in Wolong nature reserve. Journal of Integrative Plant Biology 48:1147-1153

Yue C, Chang J, Wang K, and Zhu Y. 2004. Response of clonal growth in *Phyllostachys praecox* f. *prevernalis* to changing light intensity. Australian Journal of Botany 52:171-174

Zaczek JJ, Baer SG, Hatleb JL, Brendecke WW, Schoonover JE, Williard KWJ, and Groniner JW. 2009a. Survival and genet growth and development of field-planted giant cane (*Arundinaria gigantea*) over time in southern Illinois. Castanea 74:286-299

Zaczek JJ, Baer SG, and Dalzotto DJ. 2009b. Fire and fertilization effects on the growth and spread of rhizome-transplanted giant cane (*Arundinaria gigantea*). Restoration Ecology Online Publication date 1 July 2009

APPENDIX

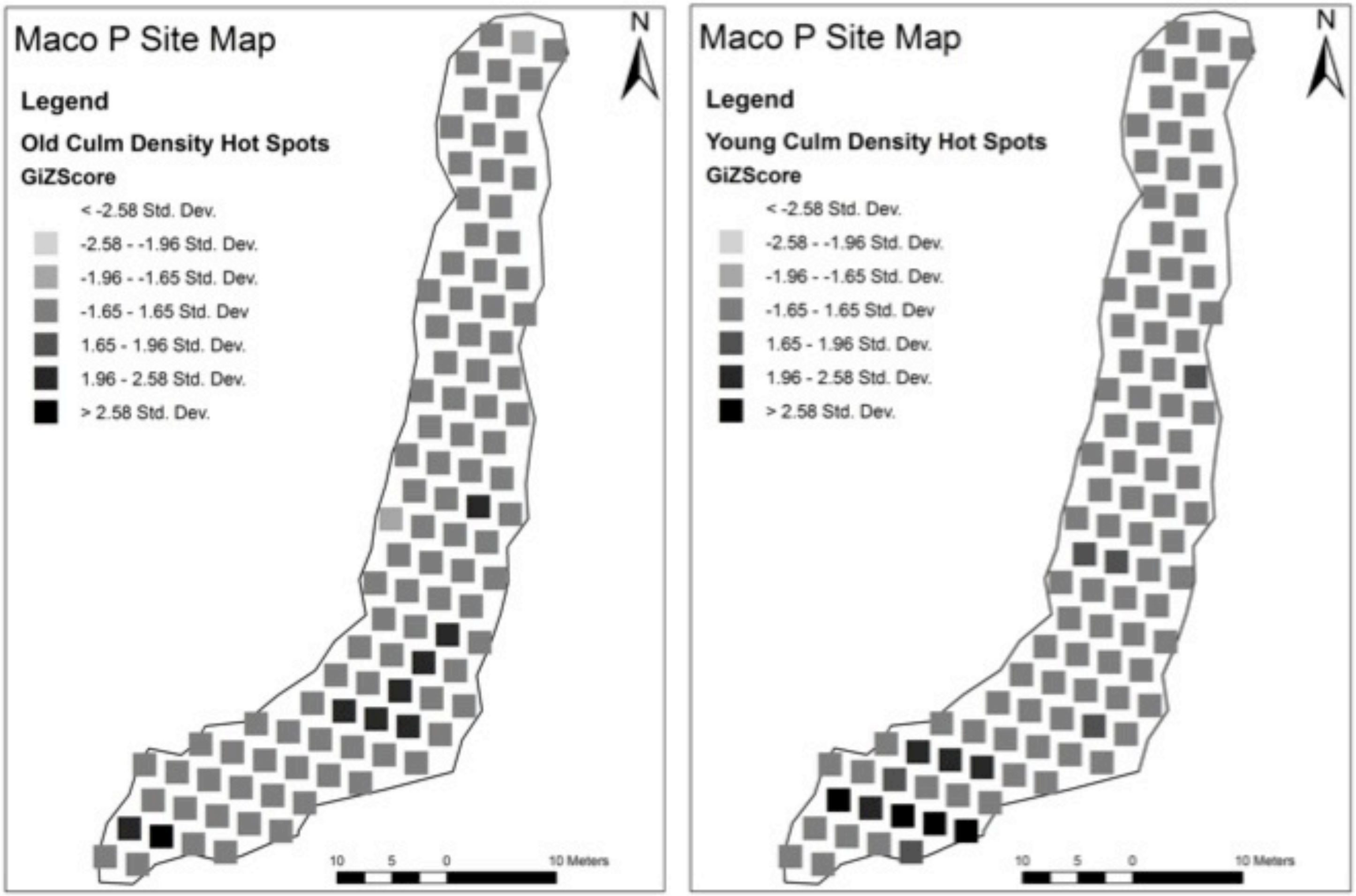


Figure 10a. Hot spot analysis for old and young culm densities in all four canebrakes. Darker squares represent areas of high density clustering

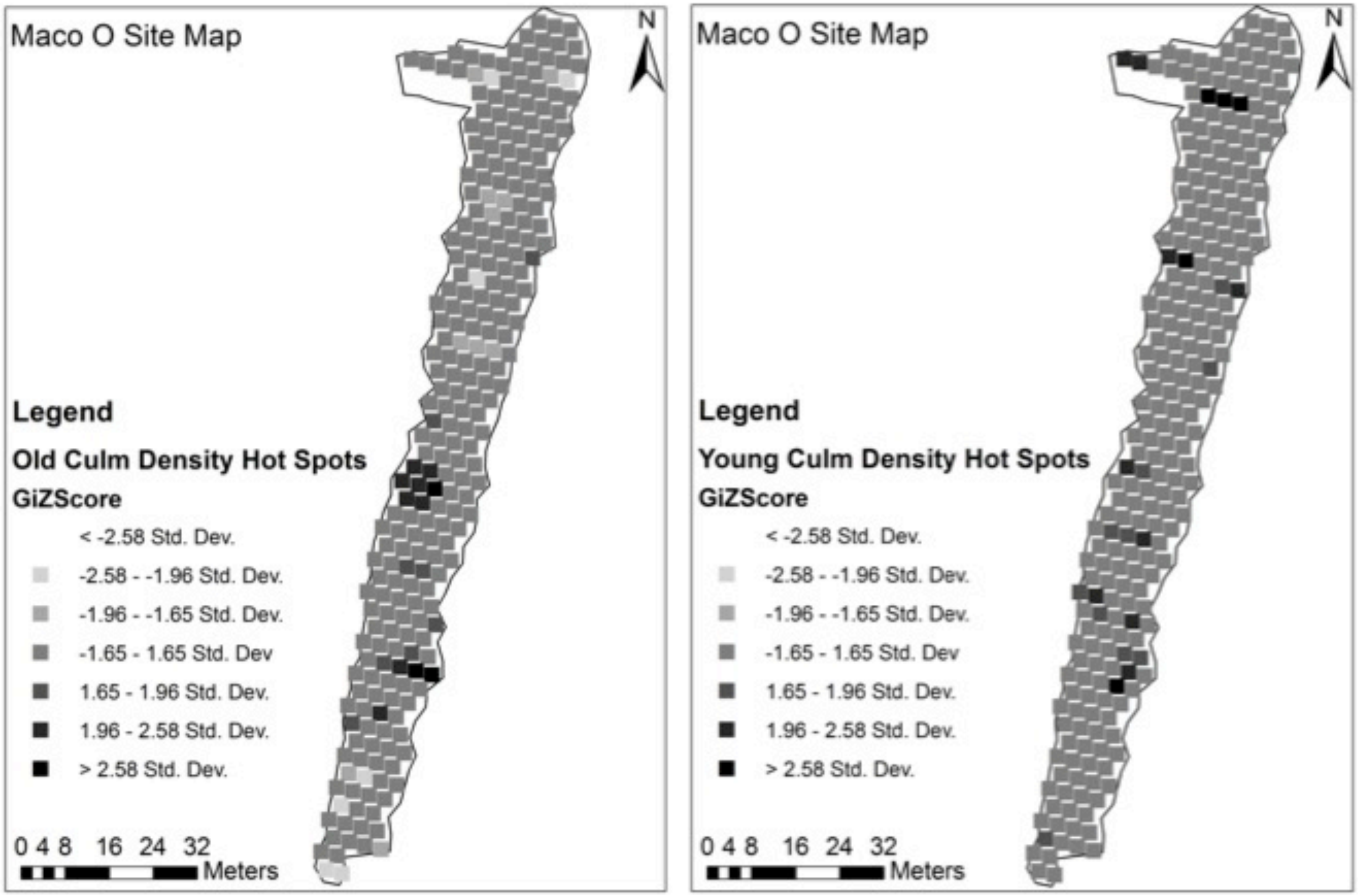


Figure 10b. Hot spot analysis for old and young culm densities in all four canebrakes. Darker squares represent areas of high density clustering

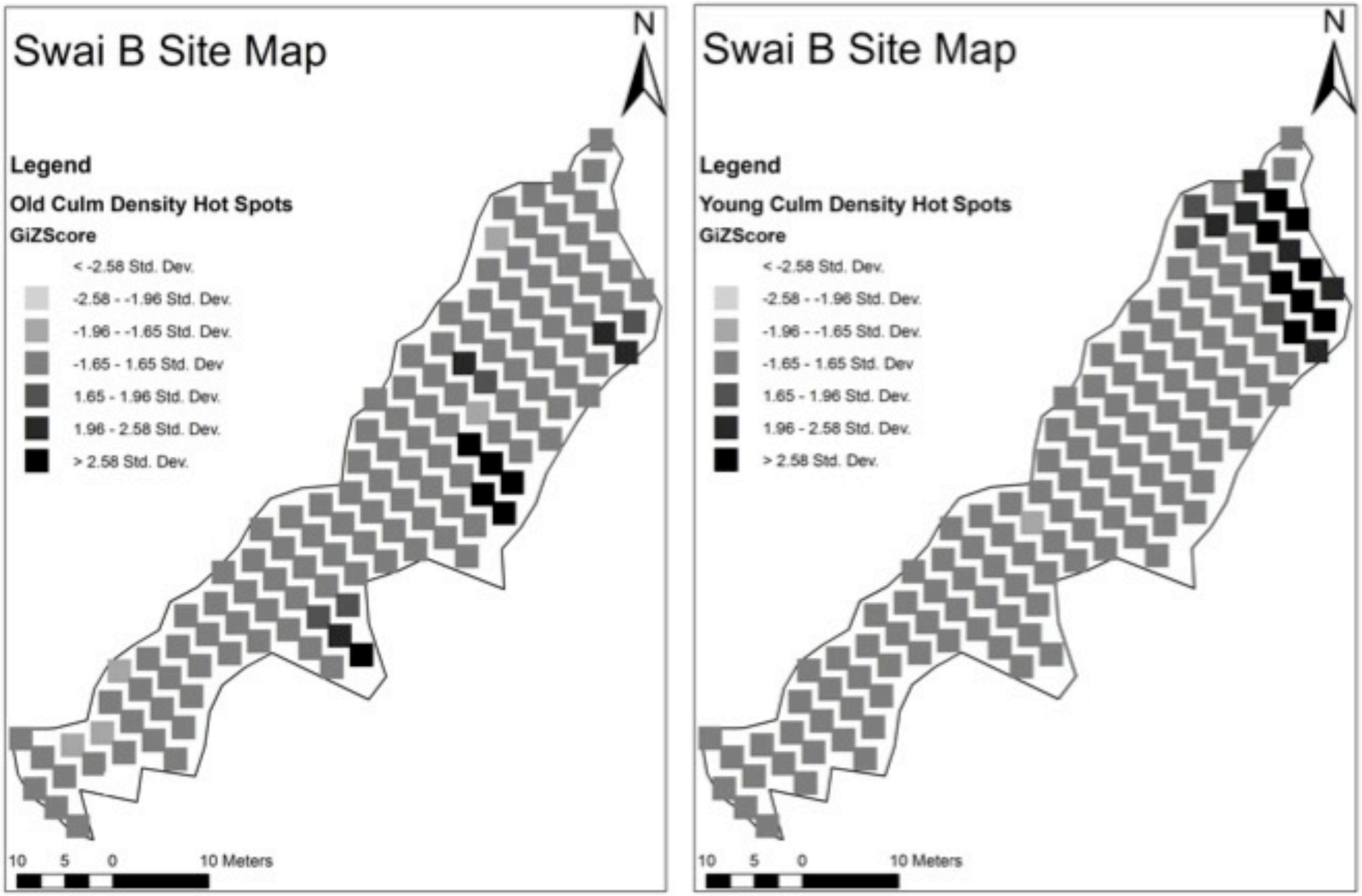


Figure 10c. Hot spot analysis for old and young culm densities in all four canebrakes. Darker squares represent areas of high density clustering

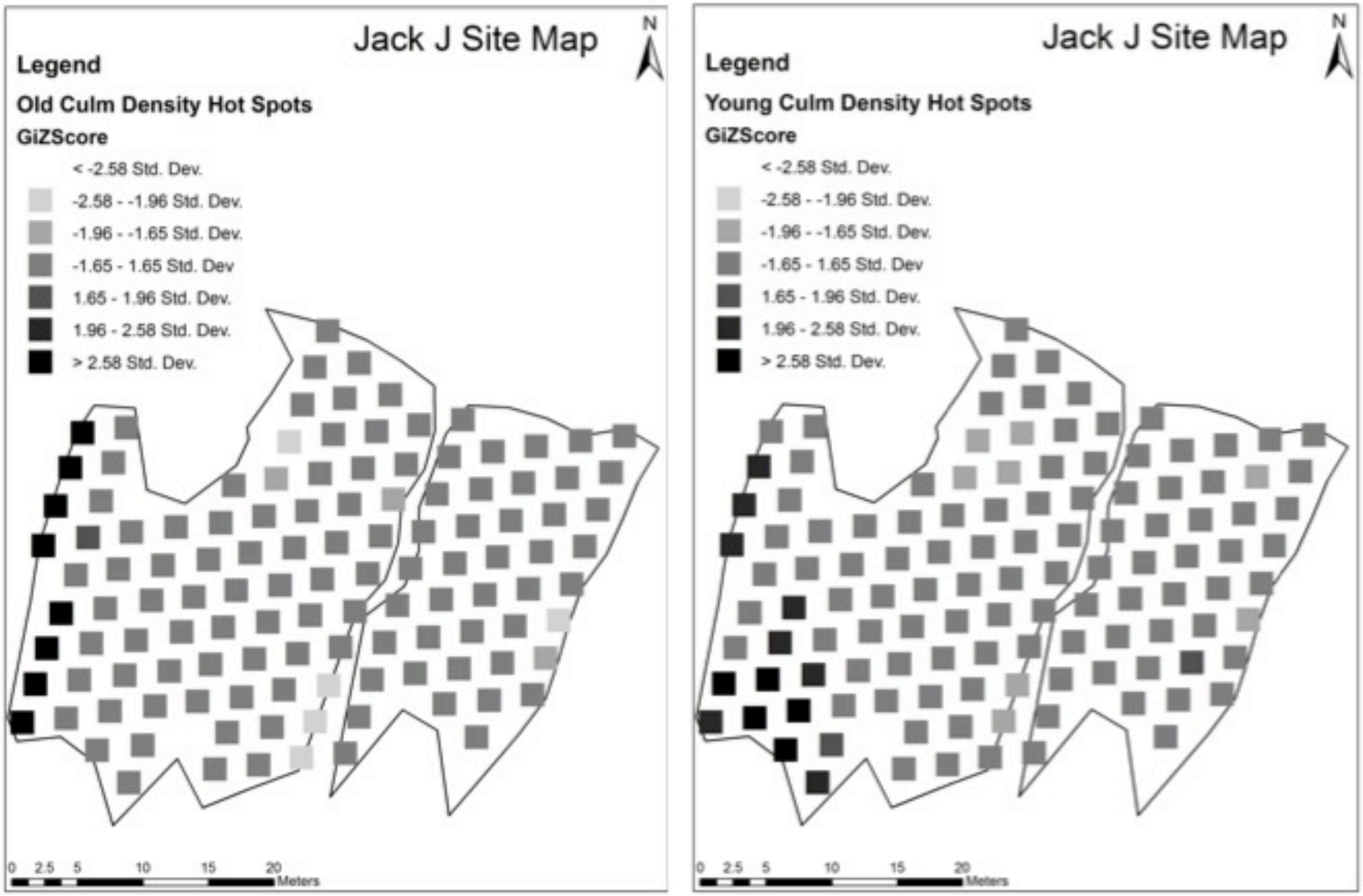


Figure 10d. Hot spot analysis for old and young culm densities in all four canebrakes. Darker squares represent areas of high density clustering

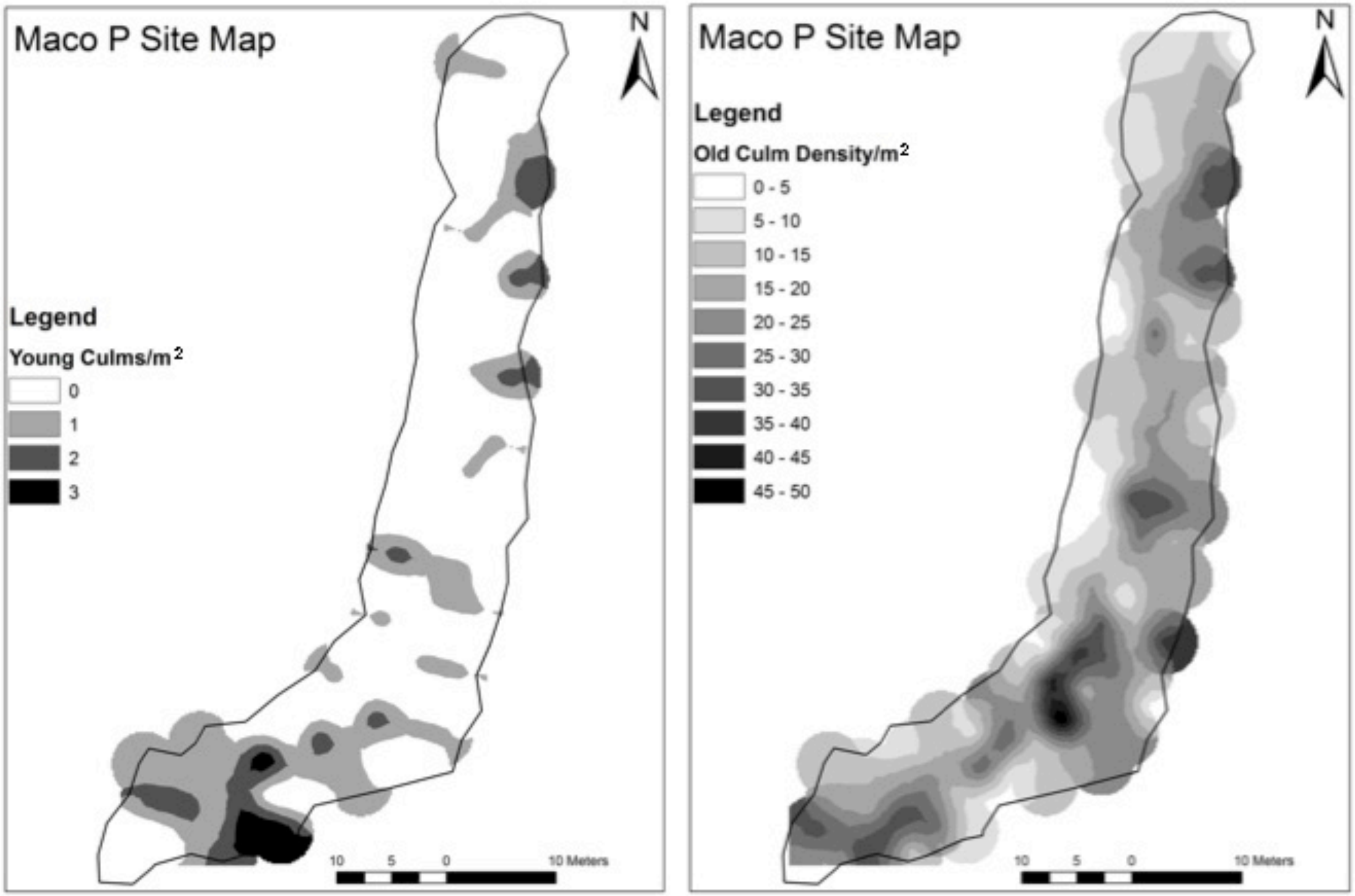
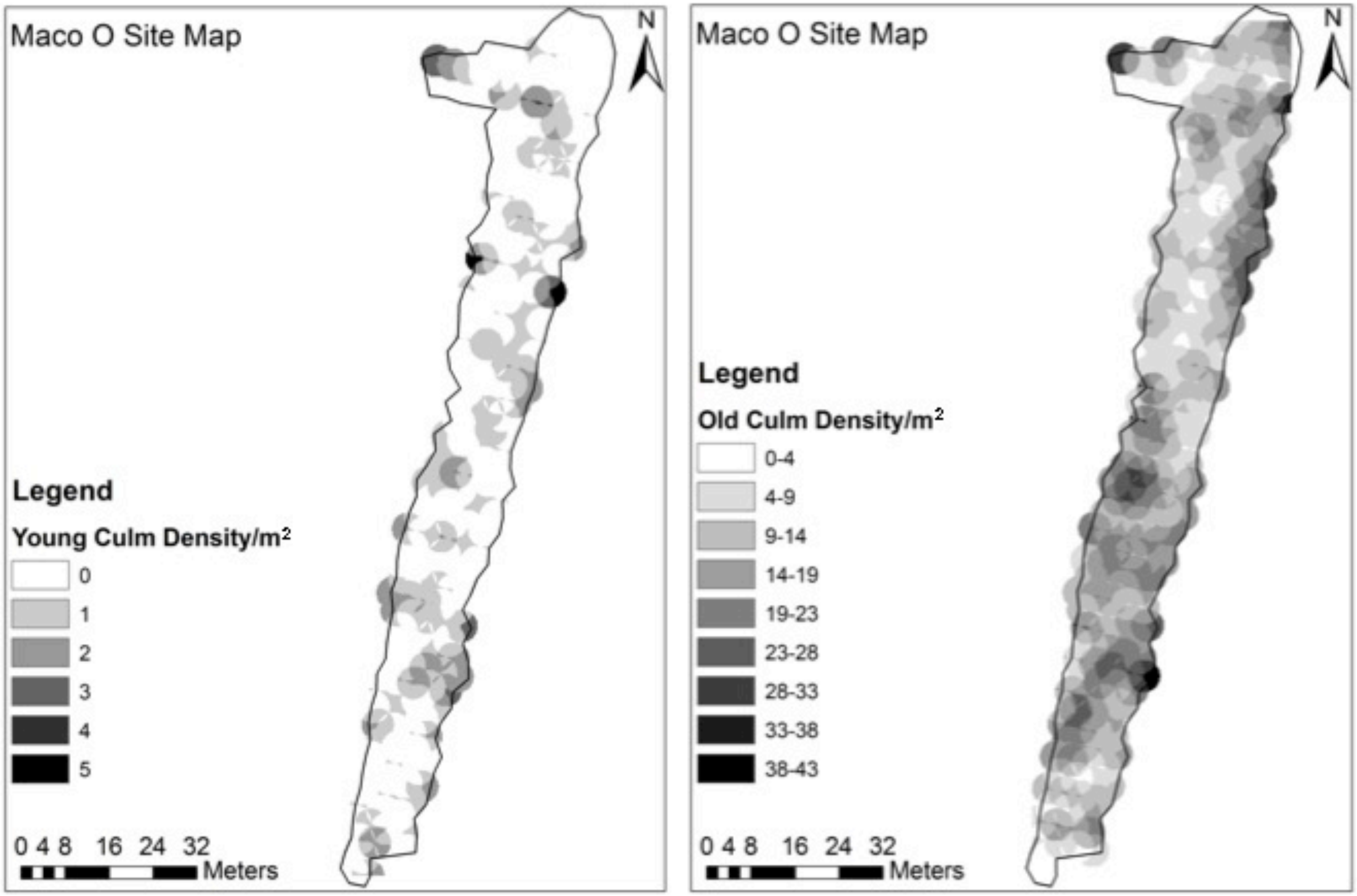


Figure 11a. Density variability for young and old culms across a canebrake site using kriging interpolation to estimate surface density in ArcInfo GIS



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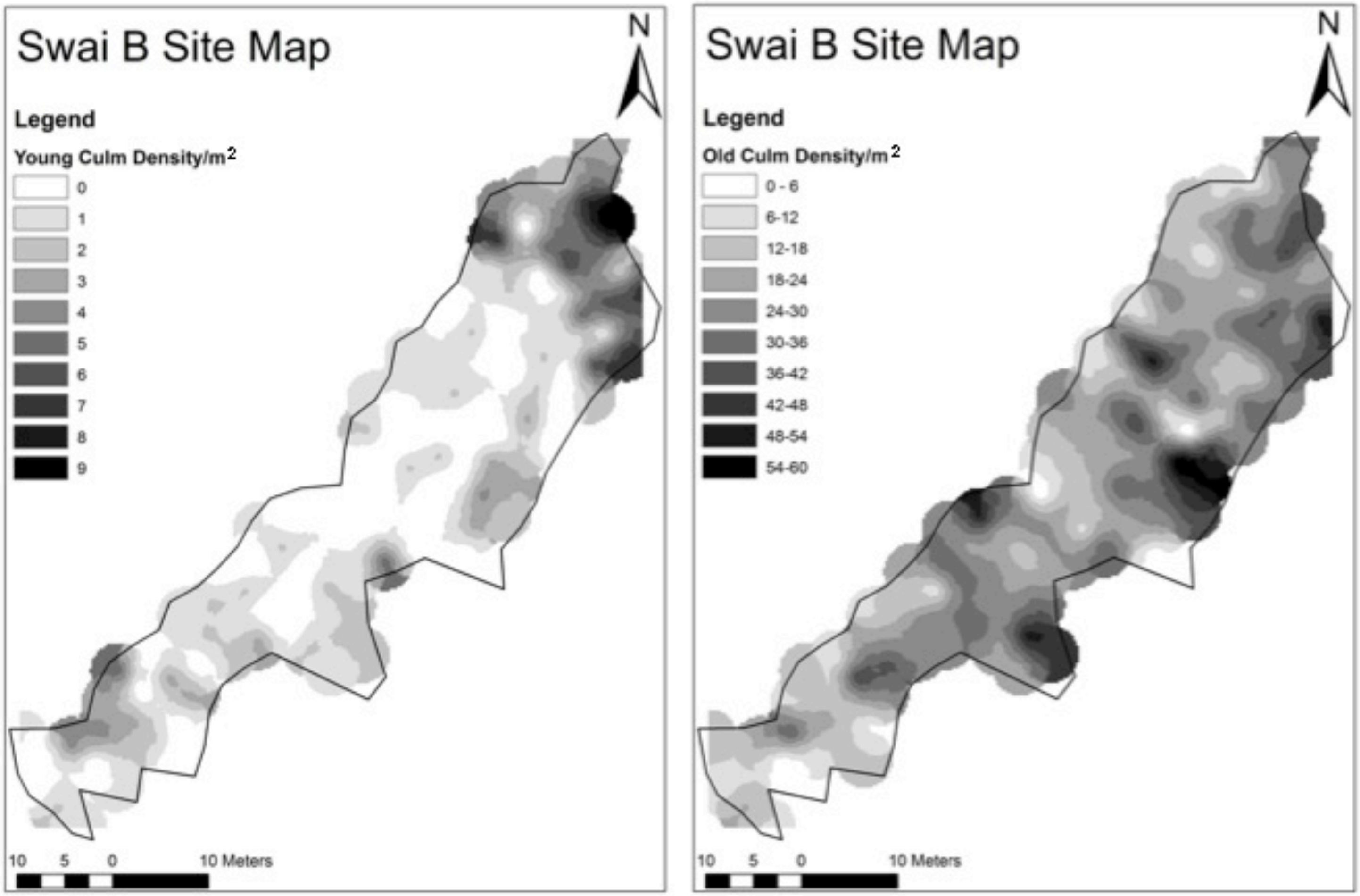

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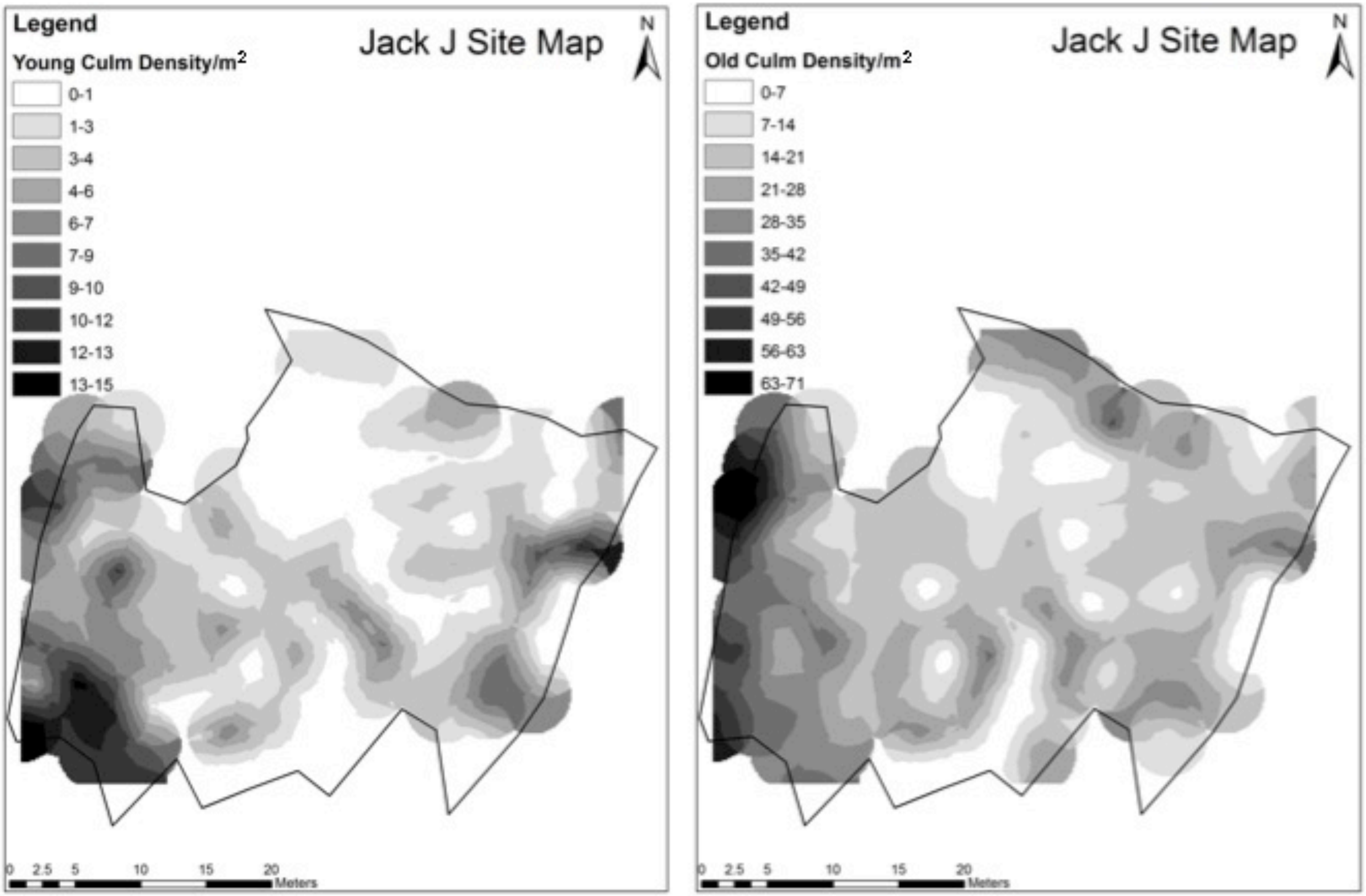

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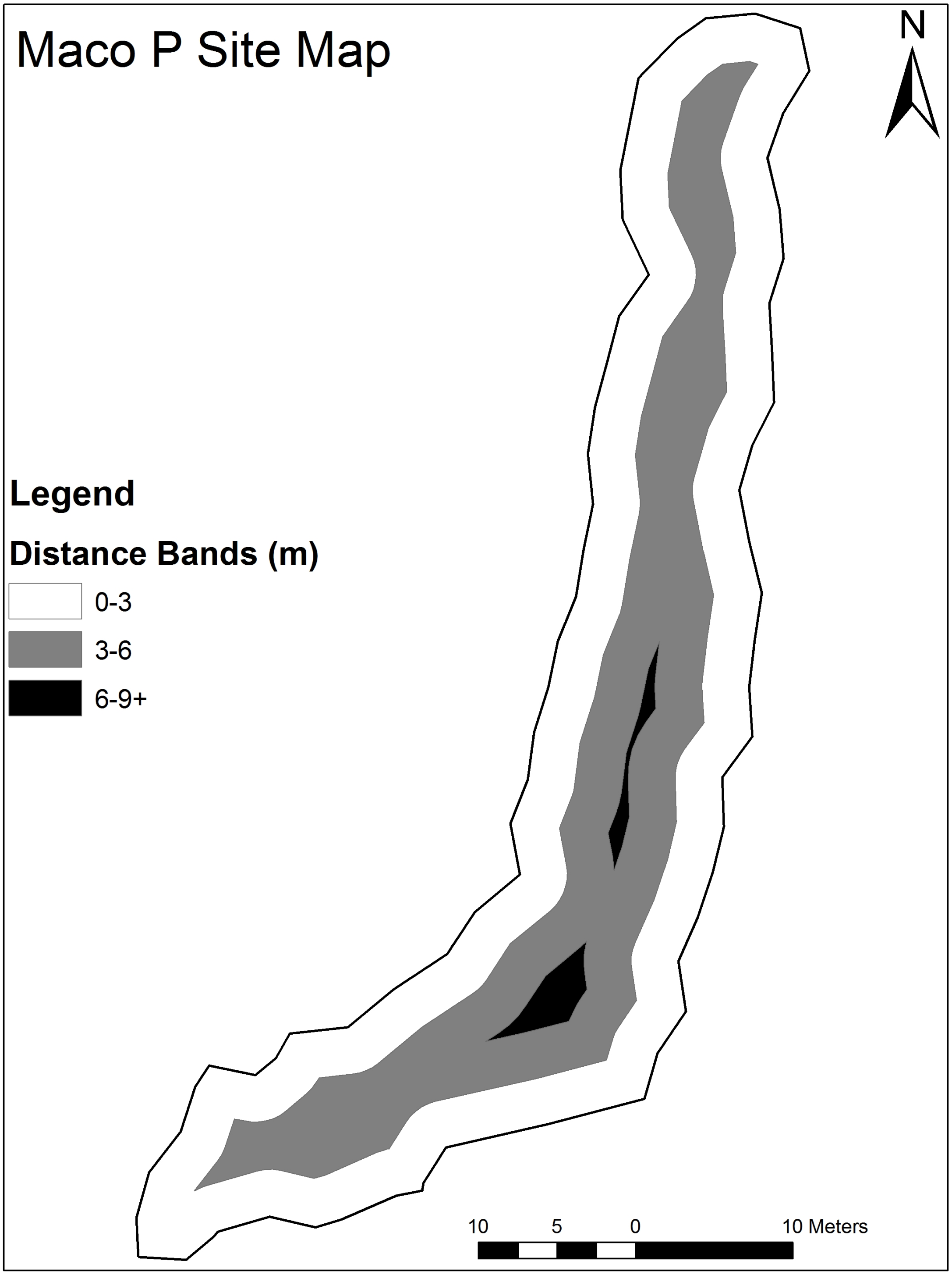

Figure 12a. Three distance band (m) maps for canebrake sites in western NC

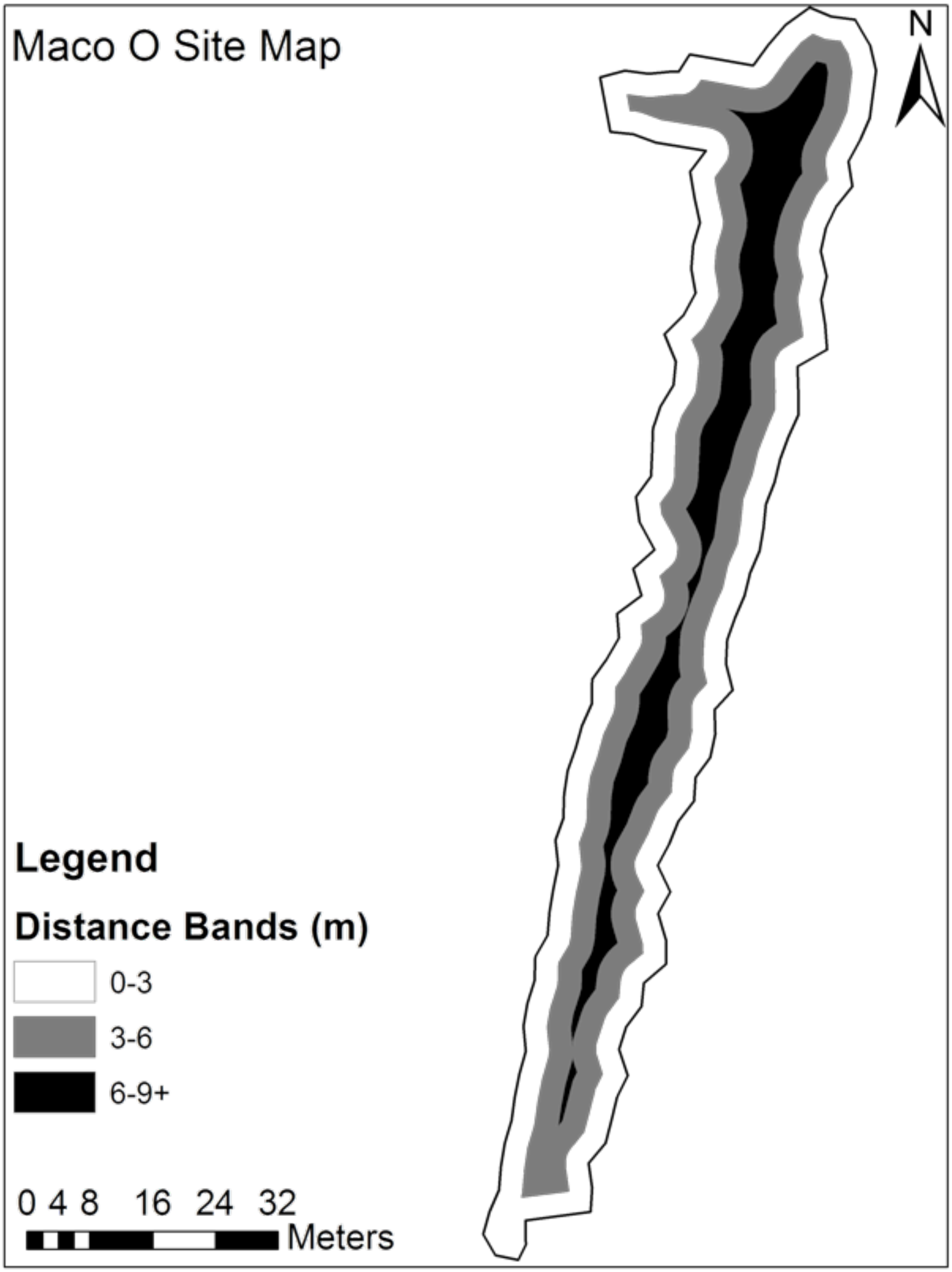

Figure 12b. Three distance band (m) maps for canebrake sites in western NC

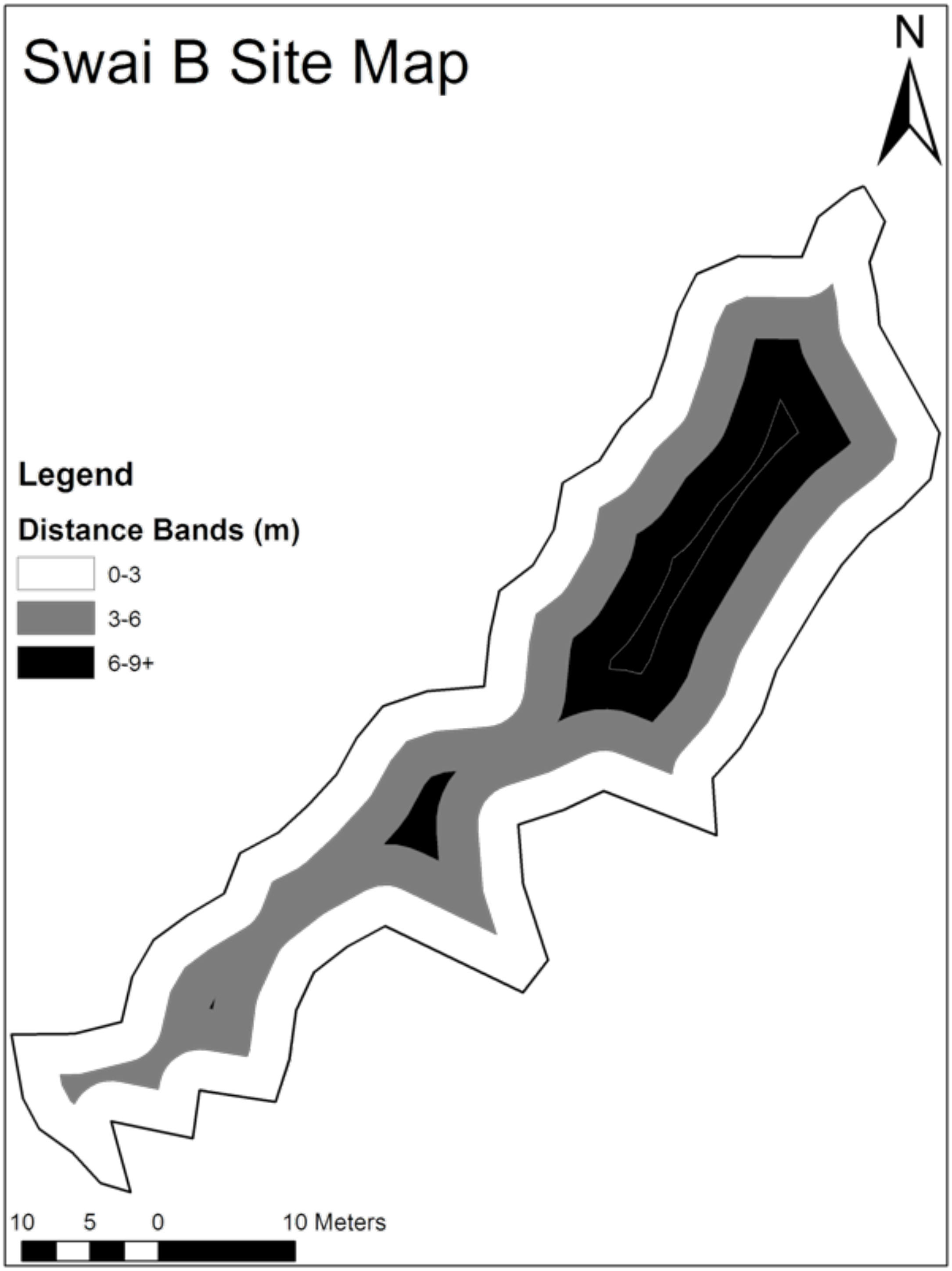

Figure 12c. Three distance band (m) maps for canebrake sites in western NC

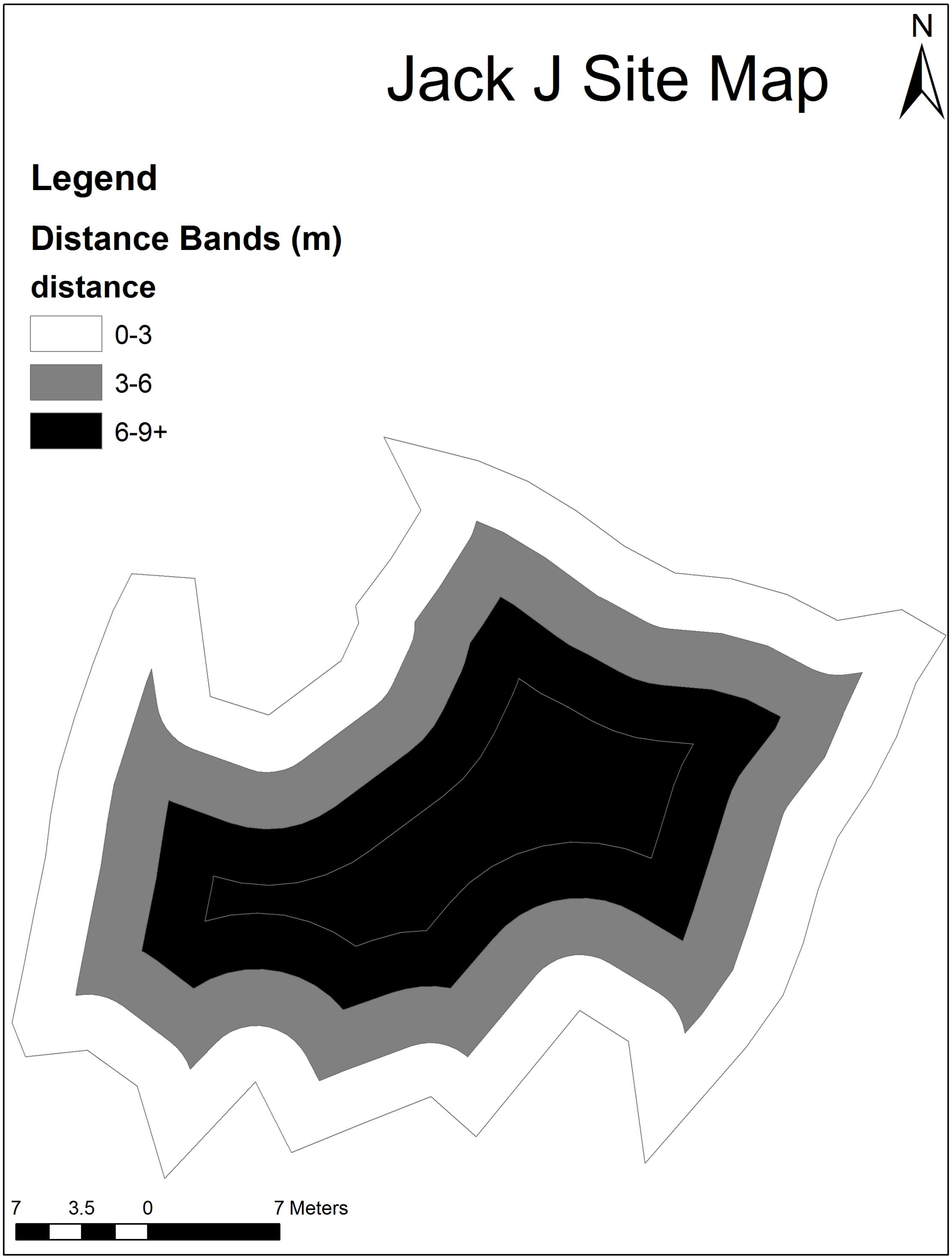

Figure 12d. Three distance band (m) maps for canebrake sites in western NC

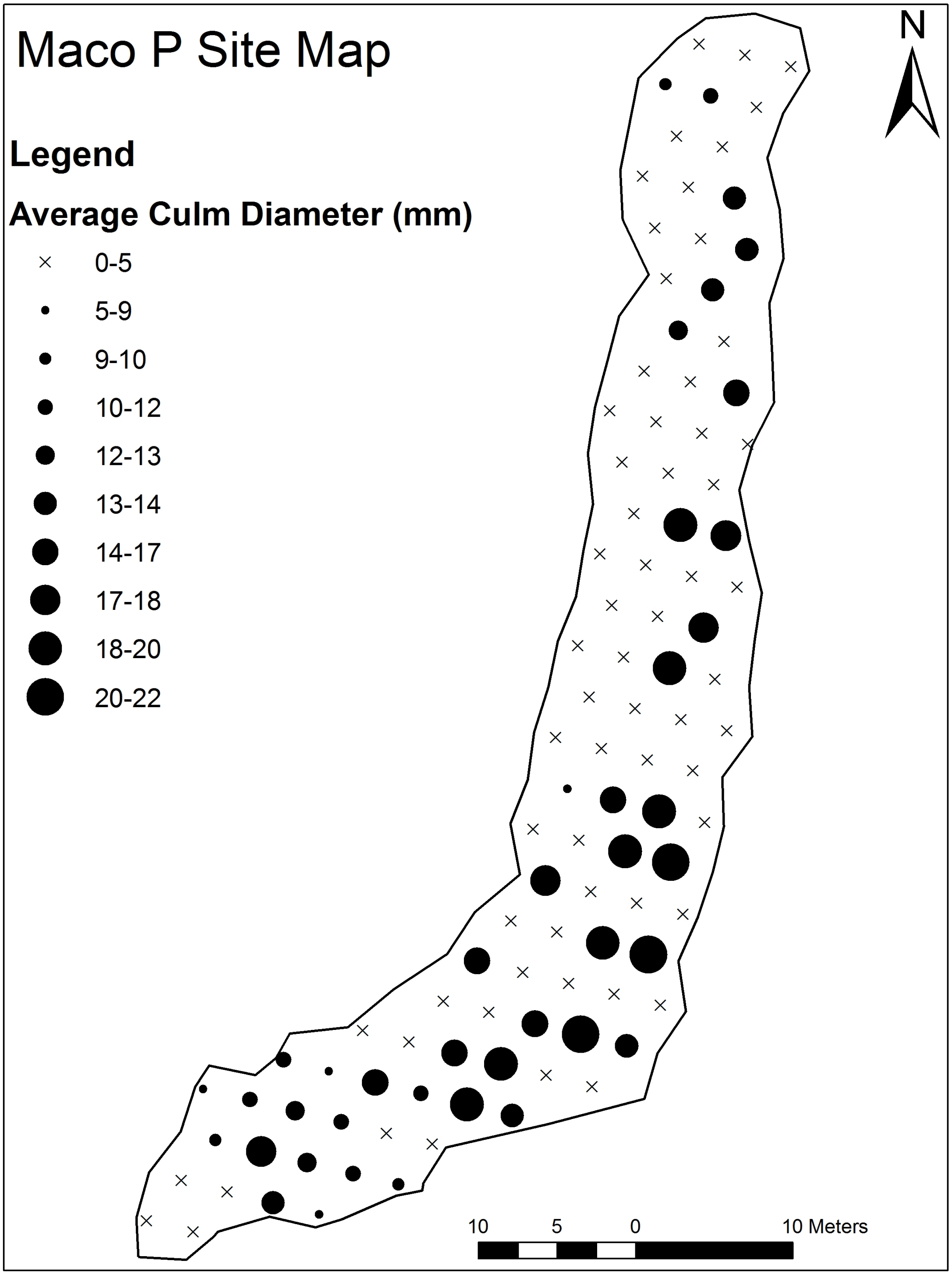

Figure 13a. Map of average culm diameter (mm) per plot for canebrake sites in western NC

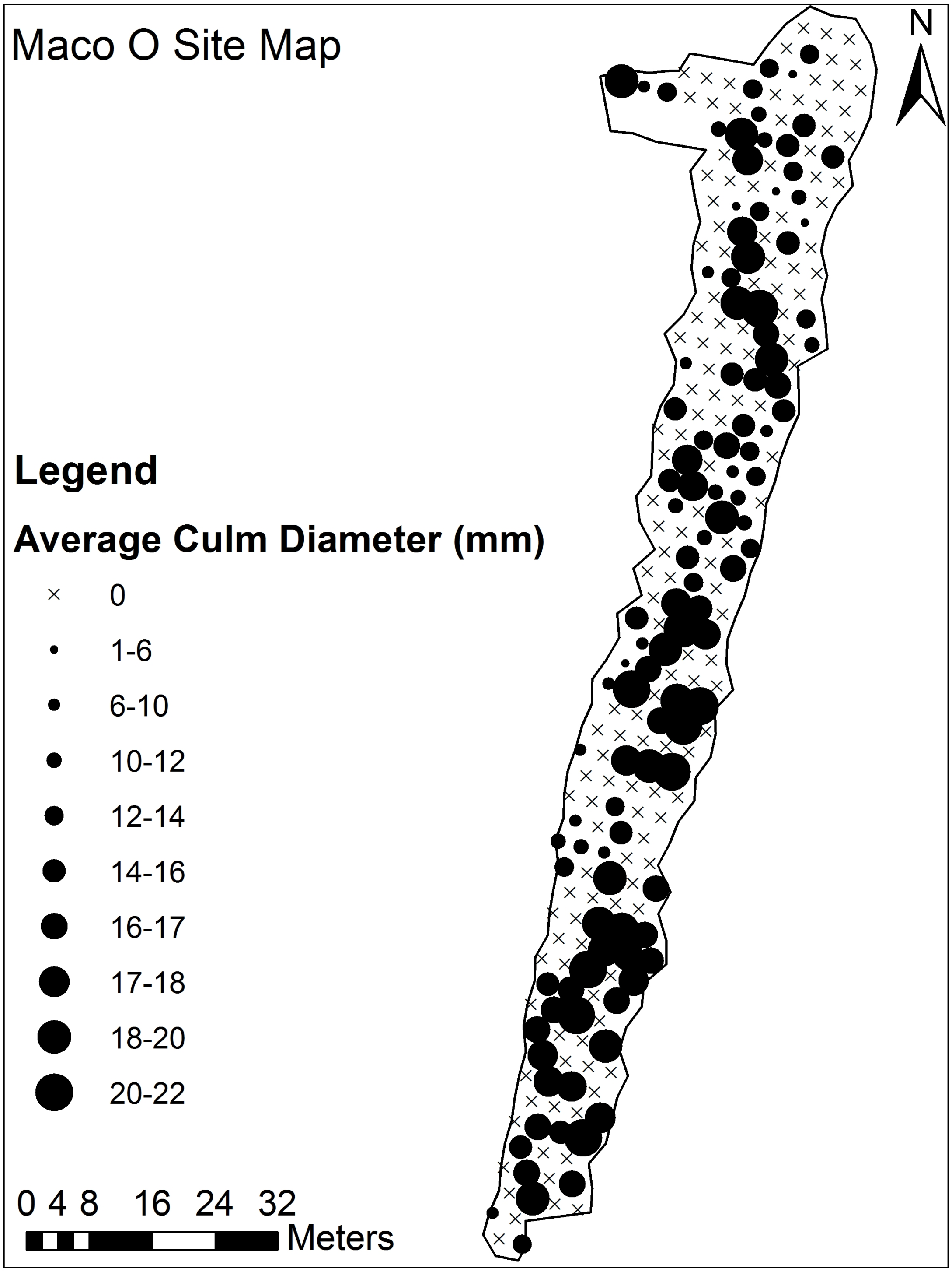

Figure 13b. Map of average culm diameter (mm) per plot for canebrake sites in western NC

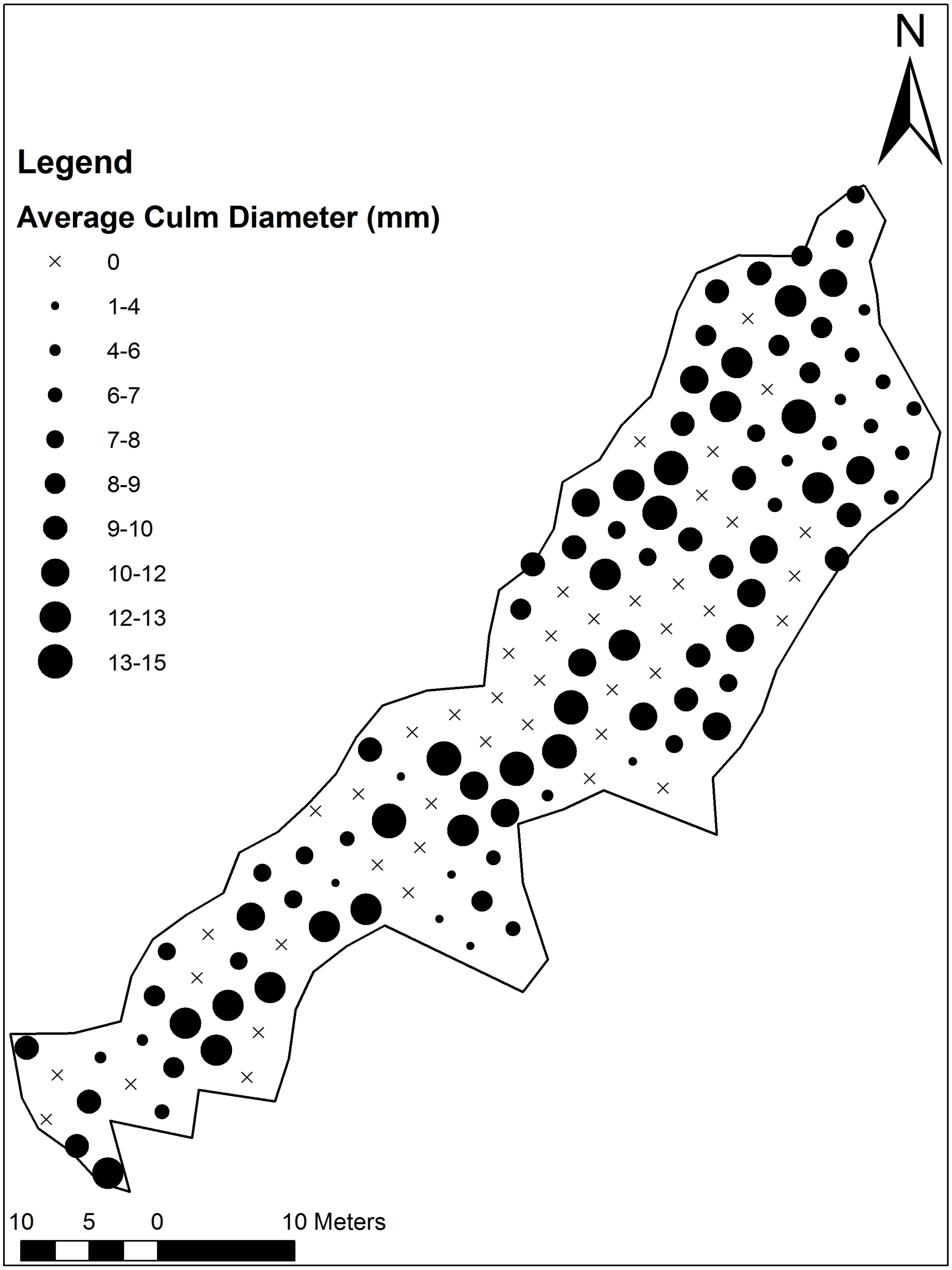

Figure 13c. Map of average culm diameter (mm) per plot for canebrake sites in western NC

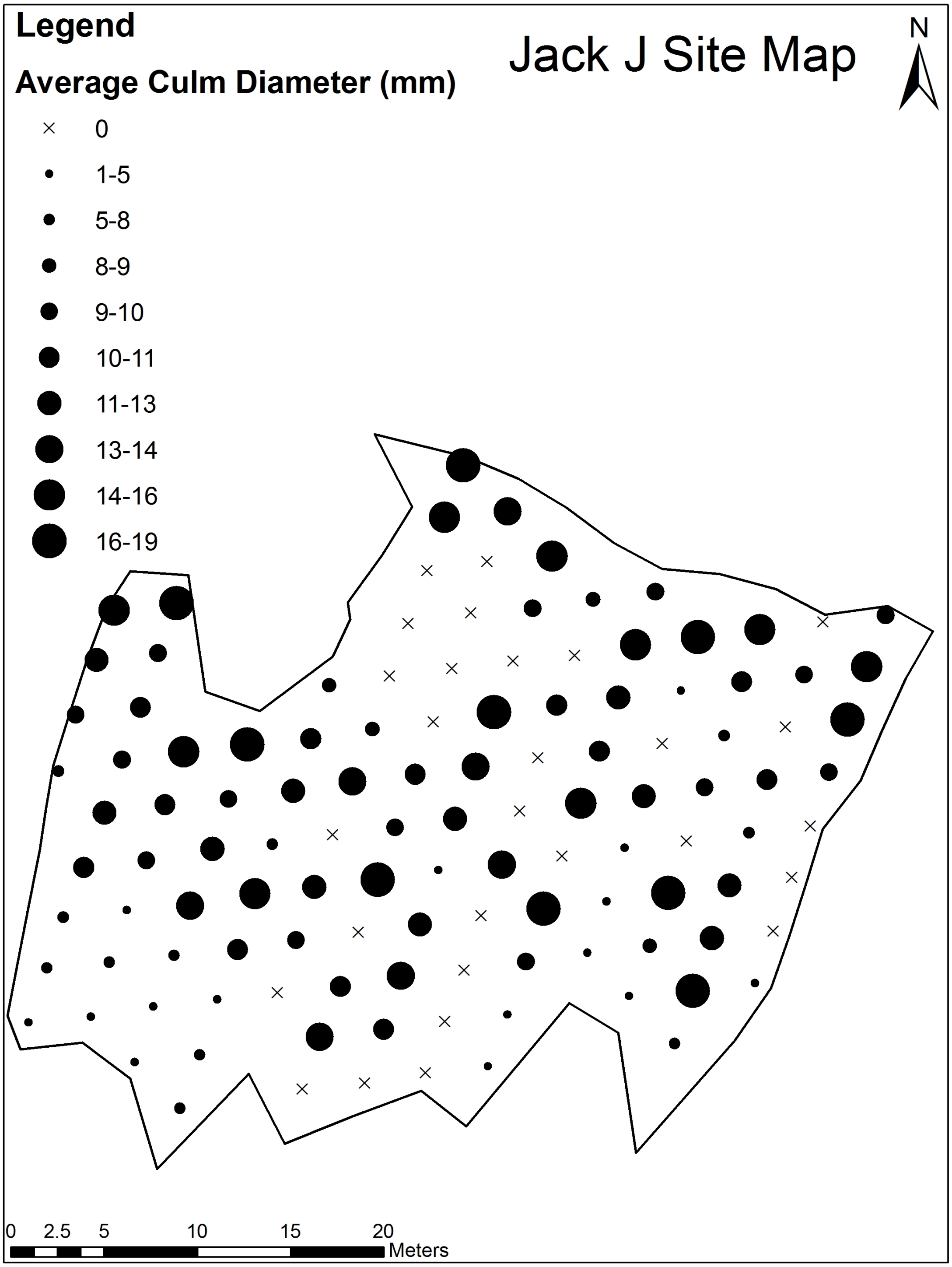

Figure 13d. Map of average culm diameter (mm) per plot for canebrake sites in western NC

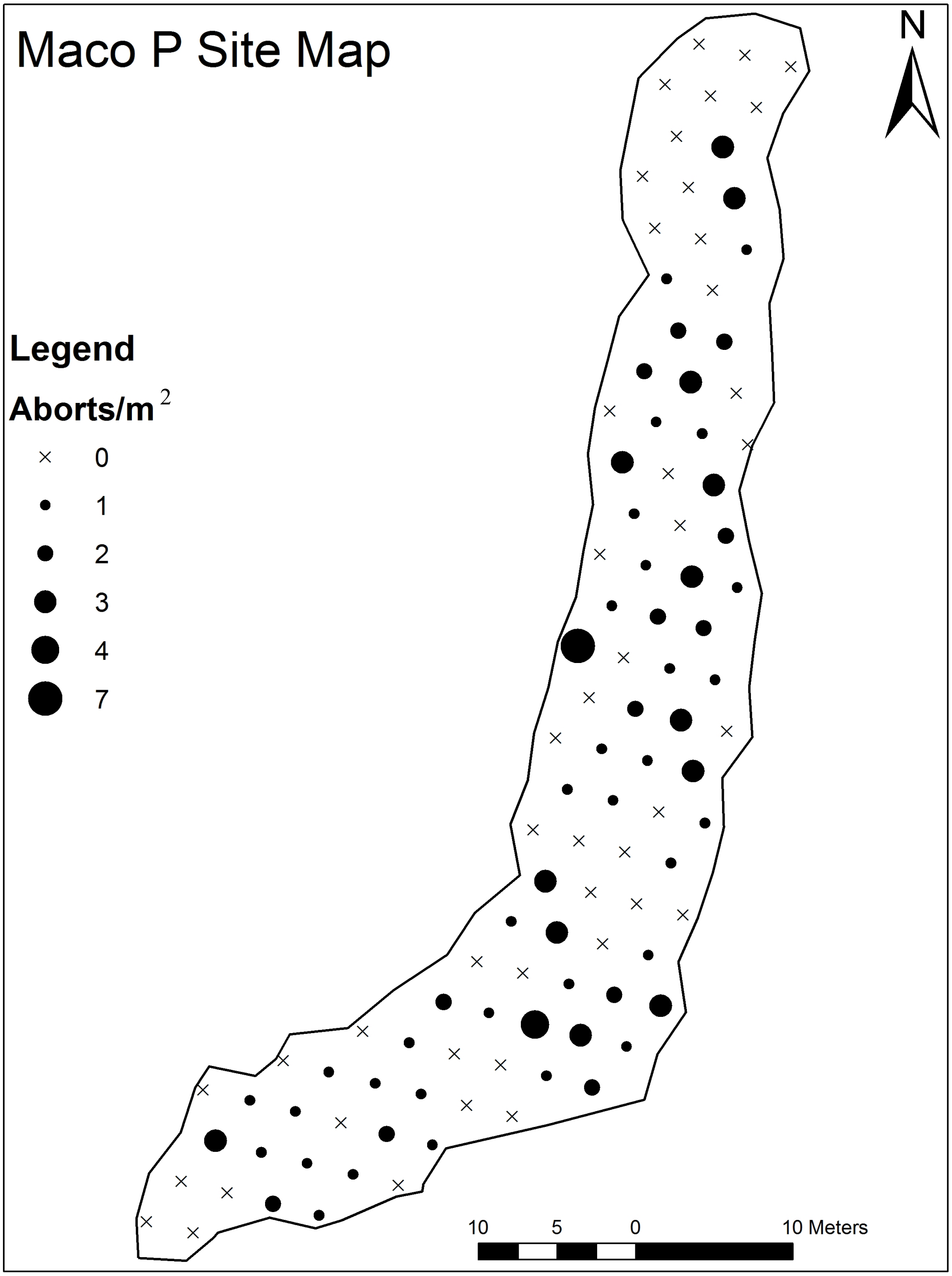

Figure 14a. Numbers of aborted culms per plot for canebrake sites in western NC

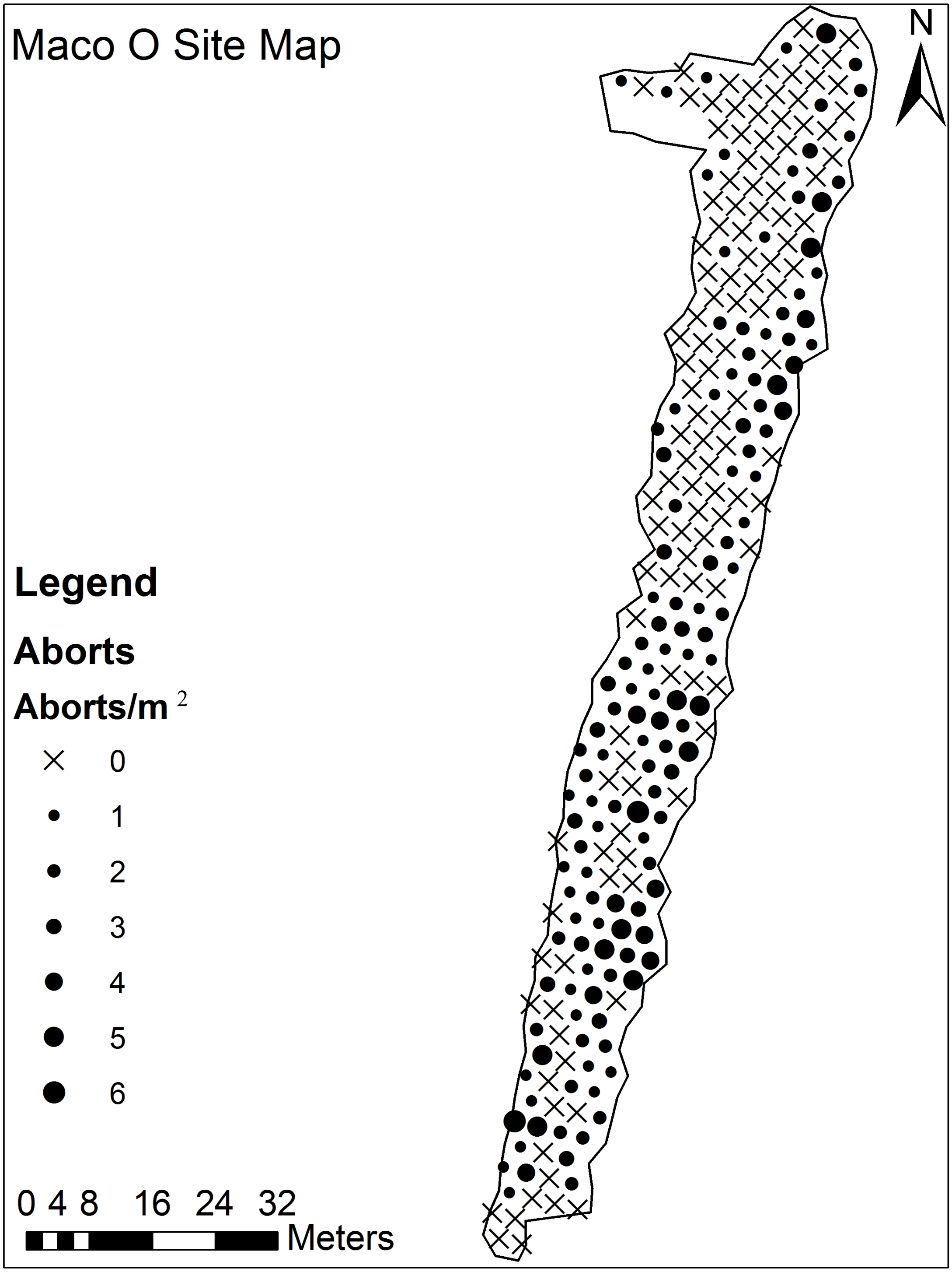

Figure 14b. Numbers of aborted culms per plot for canebrake sites in western NC

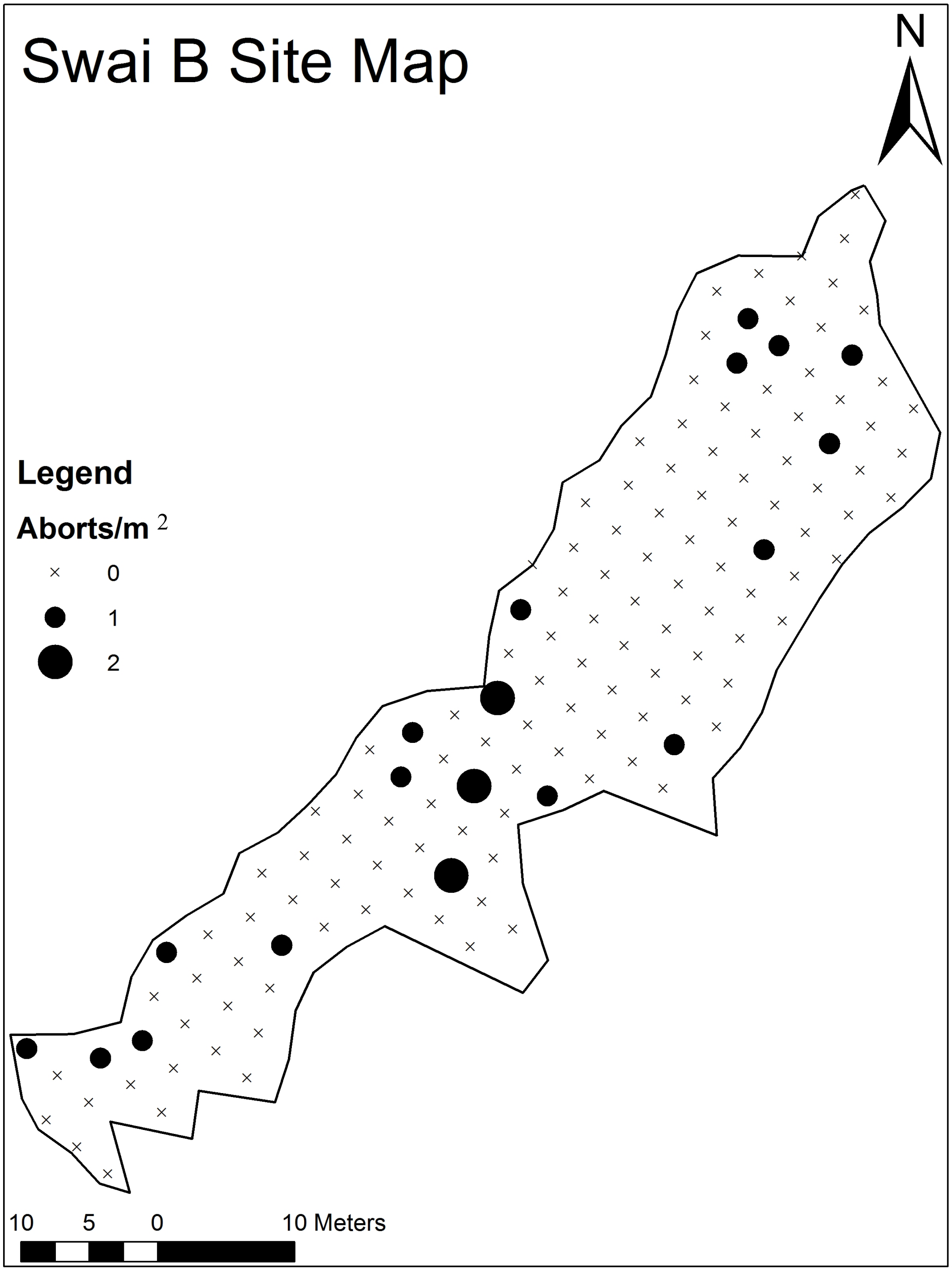

Figure 14c. Numbers of aborted culms per plot for canebrake sites in western NC

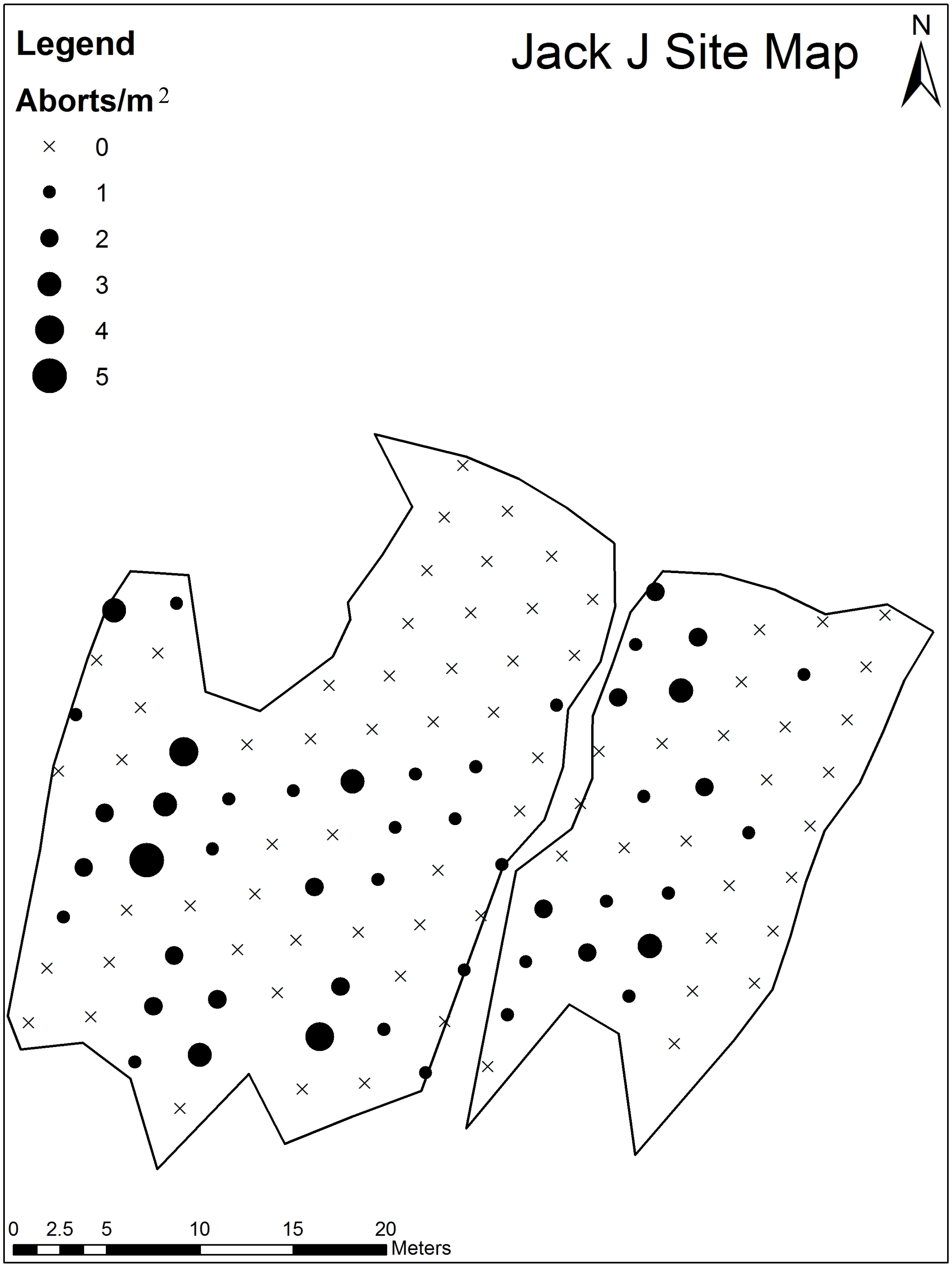

Figure 14d. Numbers of aborted culms per plot for canebrake sites in western NC

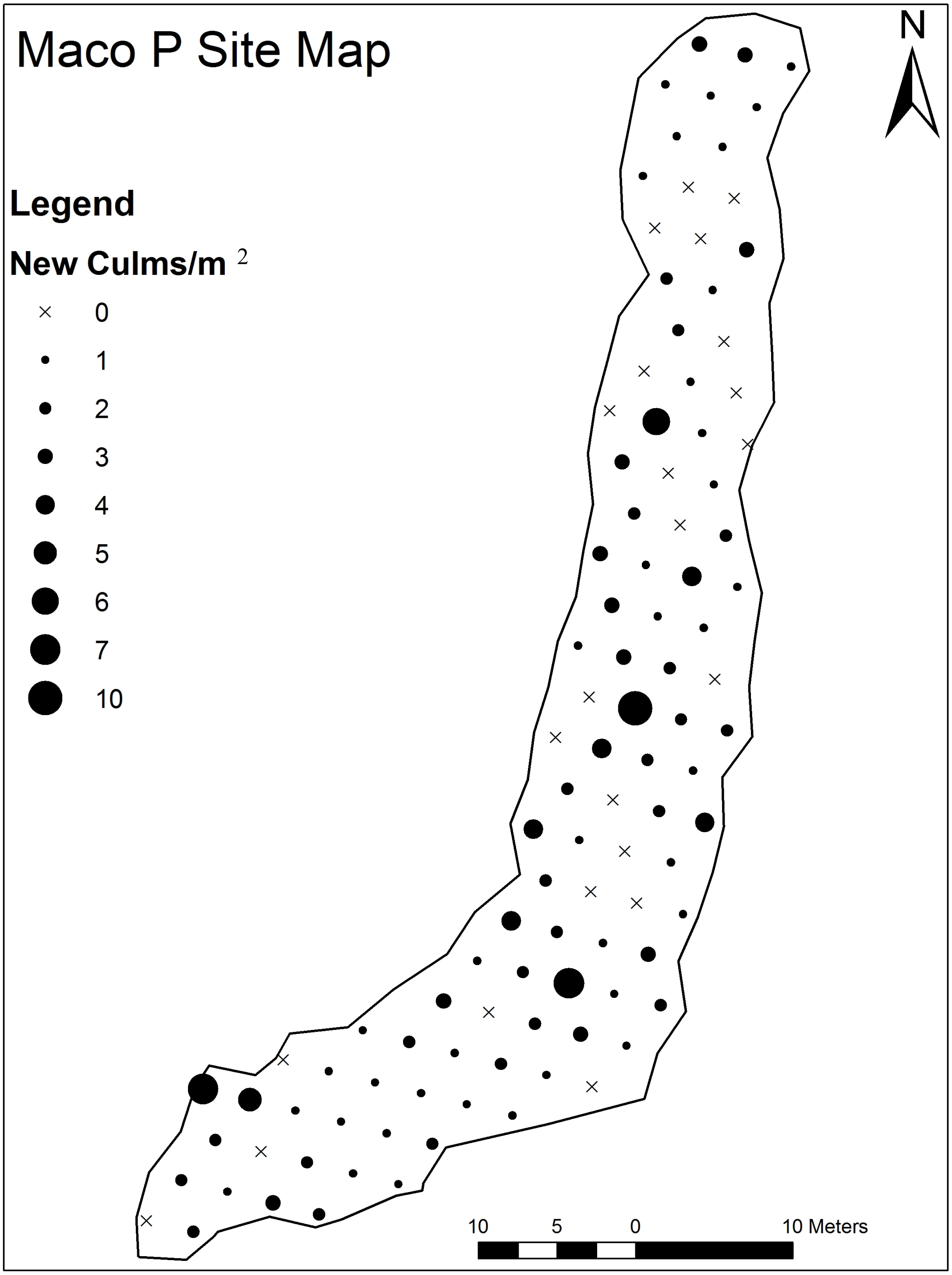

Figure 15a. Number of new culms per plot for 2 canebrake sites in western NC

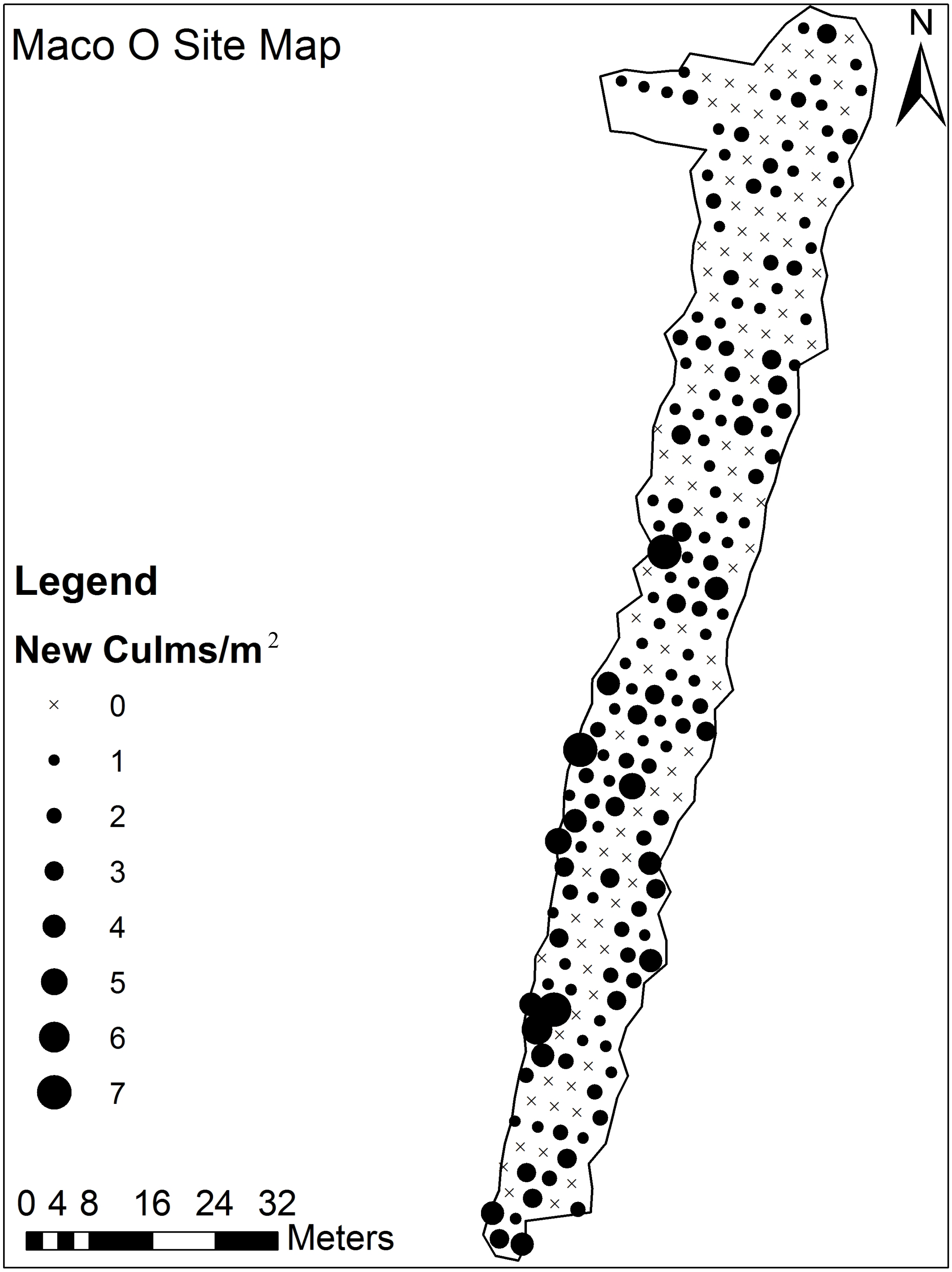

Figure 15b. Number of new culms per plot for 2 canebrake sites in western NC