Infraspecific Systematics of *Alnus maritima* (Betulaceae)  
from Three Widely Disjunct Provenances\(^1\)

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**ABSTRACT**

Two new subspecies of *Alnus maritima*, *A. maritima* subsp. *oklahomensis* from south-central Oklahoma and *A. maritima* subsp. *georgiensis* from northwestern Georgia, are described based on differences in growth habit, leaf and fruit morphology, and geographic isolation. The two new subspecies, along with subsp. *maritima* found in Maryland and Delaware on the Delmarva Peninsula, formalize the infraspecific classification of three widely disjunct populations of *A. maritima*, which have undergone considerable divergence since their isolation. Numerical analyses of 23 characters of mature trees from natural sites and 22 characters of seedlings grown in a uniform environment revealed many differences and allowed the determination of relative taxonomic distances between subspecies. Our examination of morphology, growth habit, distribution, and habitat of the three subspecies also rendered a plausible explanation for the peculiar disjunct occurrence of *A. maritima*.

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INTRODUCTION

*Alnus maritima* (Marsh.) Muhl. ex Nutt. is a rare, woody, riparian species of *Alnus* subg. *Clethropsis* (Spach) Regel found naturally in three disjunct populations in the United States (Figure 1). The occurrence of *A. maritima* in south-central Oklahoma and on the Delmarva Peninsula in Maryland and Delaware has been known for over 100 years, while the population in northwestern Georgia was not recognized until 1997 (Brian Dickman, pers. comm.). It has been postulated that subg. *Clethropsis* evolved in southern Asia, that the early ancestors of *A. maritima* entered North America via the Bering land bridge, and that the present disjunct occurrence of this species is but a remnant of a larger distribution that has given way to range restriction (Furlow 1979). The large geographic separation between the three populations suggests that genetic divergence might warrant the consideration of the three populations as subspecies.

Before the discovery of the population in Georgia, Murray (1983) attempted to treat the two known populations as separate subspecies and/or varieties. He named the Oklahoma population subsp. *metoporina* after a previously proposed (Furlow 1976), but unwarranted (Stibolt et al. 1977), specific epithet. Rather than collecting a type specimen from Oklahoma and providing a description of his own, Murray (1983) included a reference to Furlow's previous description and type specimen for *Alnus metoporina*. The major problem with Murray's treatment of the subspecies from Oklahoma was that the type specimen used and described by Furlow (1976) was collected in Delaware [*Furlow 205 (MSC!)*], not in Oklahoma. Murray's infraspecific name, *Alnus maritima* subsp. *metoporina* (Murray 1983) is therefore illegitimate according to Articles 7 and 32 of the International Code of Botanical Nomenclature (ICBN)
(Greuter et al. 1999) because no valid type specimen or description was published for the subspecies in Oklahoma.

Although the subspecies name proposed by Murray (1983) must be considered illegitimate, and although he based his conclusion on the geographical separation alone, his contention that the populations of *Alnus maritima* deserve infraspecific ranking appears correct. Here we provide evidence from a numerical analysis of morphology, growth habit, and developmental rates of both juvenile and mature plants, that significant genetic divergence has taken place among the three disjunct populations, and that these populations should therefore be considered as three subspecies. We propose the names *Alnus maritima* subsp. *oklahomensis* Schrader & Graves for the population in Oklahoma and *Alnus maritima* subsp. *georgiensis* Schrader & Graves for the population in Georgia. The population on the Delmarva Peninsula is thus *Alnus maritima* subsp. *maritima*. Also included are descriptions of the distribution and habitat of each of the three subspecies of *A. maritima* and a plausible explanation of the origin of the widely disjunct distribution of the species.

**MATERIALS AND METHODS**

The phenotypic variation and divergence of the three subspecies of *Alnus maritima* were resolved through numerical analysis of morphology, growth habit, and developmental rates of mature plants in nature (23 characters evaluated) and juvenile plants (22 characters evaluated). A mature plant was defined as any plant that bore fruit. Operational taxonomic units (OTUs) were individual plants for both age groups.

For the evaluation of mature plants, direct measurements in the field and from herbarium specimens were taken during the late summer (22 Aug. 2000 to 2 Sept. 2000) from trees across
the entire known distribution of each subspecies (Figure 2). We used only new specimens in our evaluation because we knew of no existing herbarium specimens of *A. maritima* from Georgia. The three populations (subspecies) of *A. maritima* were divided geographically into six sub-populations. Pennington Creek and Blue River sub-populations (subsp. *oklahomensis*) are located on separate waterways in south-central Oklahoma (Figure 2A). The two main sub-populations of subsp. *maritima* (SW Delmarva and NE Delmarva) are located on the two major watersheds of the Delmarva Peninsula (Figure 2B). Plants from the SW Delmarva sub-population are found on waterways that flow into the Chesapeake Bay, while plants from the NE Delmarva sub-population grow in and along waterways that flow into the Delaware Bay or Atlantic Ocean. Drummond West and Drummond East sub-populations (subsp. *georgiensis*) are separated by ~1 km within the same waterway in northwestern Georgia (Figure 2C). Forty accessible trees from each subspecies were selected randomly and measured. The identity and location of each tree were recorded according to population (subspecies), sub-population, state, county, body of water, and the longitude, latitude, and elevation measured by global positioning (GPS) equipment to an accuracy of ±5 m.

Measurements of morphology and growth habit were tree height, canopy diameter (dia.) (mean of north-south and east-west measurements), horizontal canopy area (area of an ellipse calculated from the two canopy dia. measurements), canopy surface area (surface area of a sphere calculated from the mean of the three-dimensional canopy measurements), tree shape (tree height / canopy dia.), number of trunks ≥1 cm dia. per tree, trunks per m² of canopy (# of trunks / horizontal canopy area), dia. of largest trunk at 1 m of height, leaf length, leaf width at widest axis, leaf length:width ratio, number of secondary leaf veins on one side of midrib, veins per cm of leaf length, distance from proximal end of leaf blade to its widest axis, leaf shape
(distance to widest axis / leaf length), leaf apex angle (full angle, both sides of midrib), leaf thickness (dried leaves measured at widest axis and between secondary veins), strobilus length, strobilus width at widest axis, strobilus length:width ratio, distance from proximal end of strobilus to its widest axis, strobilus shape (distance to widest axis / length), and relative health rating (1-10, 1 = worst health, 10 = best health). Leaf measurements were means of the fifth through ninth leaves from the distal end of each herbarium specimen, and strobilus measurements were means of the five largest strobili from each specimen.

An inferred phylogeny of the three subspecies was produced using the neighbor-joining method. All of the above characters were used for the analysis except canopy surface area, leaf distance to widest axis, leaf thickness, strobilus distance to widest axis, and health rating. In place of these, we analyzed timing of anthesis, presence or absence of seed wings and pistillate racemes, and prevalence of acuminate leaf apices and attenuate leaf bases. The outgroup for the analysis was *Alnus japonica* (Thunb.) Steud., an Asian species from what is considered the most primitive subgenus, subg. *Alnus* (Furlow 1979). Measurements and herbarium specimens from 10 mature *A. japonica* were used. These representative specimens were: Schrader 121, 122 (ISC), from two trees at the North Central Regional PI Station (NC7), Ames, Iowa, accession number PI 479297, cultivated from wild germplasm, collected from Japan, Kushiro-shi, Hokkaido; *Dosmann (D.)* 1, 2 (ISC), from two trees at the Arnold Arboretum, accession number 57-92, cultivated from wild germplasm, collected from Japan, Hayakita; *D. 3, 4, 5, 6* (ISC), from four trees at the Arnold Arboretum, accession number 293-83, cultivated from wild germplasm, collected from China; *D. 7* (ISC), from the Arnold Arboretum, accession number 432-73, cultivated from wild germplasm, collected from Japan, Hokkaido; *D. 8* (ISC), from the
Arnold Arboretum, accession number 1464-77, cultivated from wild germplasm, collected from Japan, Honshu.

One soil core to a depth of 30 cm was collected at the base of each tree or localized group of trees. Samples were analyzed for plant-available concentrations of nitrate (N, by Colorimetric), phosphorus (P, by Olsen), potassium (K, with NH$_4$OAc), calcium (Ca, with NH$_4$OAc), and magnesium (Mg, with NH$_4$OAc), and for soil pH and percentage organic matter (by combustion) by the Soil and Plant Analysis Laboratory, Iowa State University, Ames, Iowa. The soil water table (vertical distance from the soil-trunk intersection to the visible level of water in the adjacent waterway) was measured at the base of each tree. Local climatic conditions were also recorded for the three provenances. The percentage of daily shade caused by competing trees and local landforms was estimated for each plant. Annual mean minimum and maximum temperatures, mid-winter minimum (the lesser of January or February means per year), mid-summer maximum (the greater of July or August means per year), and annual precipitation were calculated from data recorded from 1981 to 1990 at weather stations in Ardmore, Oklahoma; Rome, Georgia; and Denton, Maryland, and compiled by the National Climate Data Center (2001).

Measurements of juvenile plants were adapted from previous research during which we evaluated the growth and morphology of seedlings in a greenhouse up to 18 weeks after germination (Schrader and Graves 2000a). Measurements were leaf width at widest axis (newest fully expanded leaf), leaf length from the apex to the petiole, leaf length:width ratio, surface area of all leaves longer than 1 cm (per plant), leaf area ratio (Harper 1977), dry leaf weight (per plant), specific leaf weight (dry weight divided by surface area), bullate rating (rating of 1 or 2 when <50% or ≥50% of leaves had puckered surfaces, respectively), stem thickness at the
cotyledonary node, stem curvature rating (1 if the stem was uniformly upright, 2 if the primary stem was distinctly curved or twisted), stem deviation from vertical (deviation from a line perpendicular with the upper plane of the pot), length of the internode directly basipetal to the newest fully-expanded leaf, shoot length (length of the primary stem from the cotyledonary node to the apex), number of leaves plus axillary shoots longer than 1 cm, leaves plus axillary shoots per cm of stem, dry weights of root and shoot systems and the root:shoot dry weight ratio, net assimilation rate and relative growth rate for weeks 12 through 18 (calculated as described by Harper 1977), and simple growth rate (change in mean plant dry weight from week 12 to week 18 divided by the number of days of growth) (Schrader and Graves 2000a).

Data were analyzed by using the general linear models (GLM) procedure and the least significant difference (LSD) option of SAS/STAT software, Version 6.12 (1989-96). A correlation procedure was used to examine if subspecies characteristics were consistent between juvenile and mature plants. Analysis of covariance was performed to determine the importance of climatic and edaphic factors that may have contributed to the divergence of the three subspecies. Cluster analyses and dendrograms were used to assess the relative taxonomic distances between the three subspecies, between sub-populations within the subspecies, and to test the predictive power of the taxonomic characters. All characters were used for cluster analyses except for the health rating of mature plants, which might be considered too dependent on environmental influences. Centroid, UPGMA (Unweighted Pair-Group Method using arithmetic Averages), and Ward's clustering analyses were performed using JMP software, Version 3.2.6 (1989-99), and neighbor-joining cladograms were produced using PHYLIP (Phylogeny Inference Package), Neighbor software (Felsenstein 1995). Taxonomic distance for UPGMA cluster analyses was defined as the average distance between pairs (one in each cluster)
of observations (SAS Institute Inc. 2000) or between individual entities when only two were
joined. Taxonomic distances for neighbor-joining analyses were Euclidean distances (Sneath
and Sokal 1973). Data were standardized and unweighted in all cluster analyses.
Standardization consisted of dividing the differences for each variable by its standard deviation
(SAS Institute Inc. 2000).

Plant descriptions were organized according to Radford et al. (1974). Latin diagnoses
were translated according to Stearn (1983).

RESULTS

Character Means

Numerical analysis revealed many differences in the morphology, growth habit, and
developmental rates of the three subspecies of *Alnus maritima*. Of the 23 characters measured
on mature plants in nature, six showed differences in mean separation between all three
subspecies, 14 had differences between one subspecies and the other two, and only three
character traits were statistically similar for all three subspecies (Table 1).

Mature trees of subsp. *georgiensis* were taller than those from the other two subspecies,
but subsp. *oklahomensis* had the largest canopy diameter and horizontal canopy area (Table 1).
The composite measurement of tree shape (height / dia.) was greatest for subsp. *georgiensis* and
least for subsp. *oklahomensis*. The canopy surface area was larger for subspp. *oklahomensis* and
*georgiensis* than it was for subsp. *maritima*. Subspecies *oklahomensis* had fewer trunks per m²
than did the other two subspecies, but mean diameter of its trunks was larger than that of subsp.
*maritima*. Trees from subsp. *maritima* were the smallest for every measurement of tree size (tree
and trunk characters in Table 1) except the number of trunks, which showed no differences, and trunks per m$^2$, which was highest for subsp. *maritima*.

The greatest differences in leaf morphology were between subsp. *oklahomensis* and the other two subspecies (Table 1). The leaves of *oklahomensis* were longer and narrower than were those of the other two subspecies, giving subsp. *oklahomensis* the greatest leaf length:width ratio. Plants from Oklahoma had the greatest number of secondary veins per leaf, the lowest composite measurement for leaf shape, and the smallest leaf apex angle. Leaves of subsp. *georgiensis* had a greater leaf length:width ratio than did subsp. *maritima* and greater leaf thickness than the other two subspecies (Table 1).

The strobili of subsp. *georgiensis* were shorter than those of the other two subspecies, and strobili of subsp. *oklahomensis* were narrower with a greater length:width ratio than found in the other two subspecies (Table 1). Strobili from subsp. *maritima* had a lower distance to widest axis and lower composite measurement for strobilus shape than did strobili of the other two subspecies. Finally, the mature plants from subspp. *oklahomensis* and *maritima* were rated as healthier than those of subsp. *georgiensis* (Table 1).

An earlier study by Schrader and Graves (2000a) demonstrated that morphology, growth habit, and developmental rates of 18-week-old seedlings also differed among subspecies. Seedlings of subsp. *oklahomensis* have thicker and straighter stems than do seedlings of the other two subspecies (Table 2). As was observed with mature trees, seedling leaves of subsp. *oklahomensis* are longer and narrower than are leaves from the other two subspecies (Table 2). Leaves of subspp. *georgiensis* and *maritima* are more bullate than leaves of subsp. *oklahomensis* (Schrader and Graves 2000a).

After 18 weeks of growth, seedlings of subsp. *georgiensis* are taller than seedlings from
the other two subspecies and have longer internodes than do seedlings of subsp. *oklahomensis* (Table 2). Seedlings of subsp. *oklahomensis* are densely foliated. They have more leaves and axillary shoots and more leaf surface area per plant than do seedlings from the other two subspecies (Table 2). Compared to seedlings from subsp. *georgiensis*, seedlings from subspp. *oklahomensis* and *maritima* have more leaves and shoots per unit length of primary stem and a greater leaf area ratio (Table 2). Seedlings from subspp. *oklahomensis* and *georgiensis* have greater simple growth rates and leaf, root, shoot, and total dry weights after 18 weeks than seedlings from subsp. *maritima* (Table 2). Seedlings from subsp. *oklahomensis* have a greater root:shoot ratio than plants from the other two subspecies, while plants from subsp. *georgiensis* have the greatest specific leaf weight (Schrader and Graves 2000a).

*Cluster Analyses*

In the most basic of our cluster analyses, the character means recorded in Tables 1 and 2 were used to resolve the relative taxonomic distances of the three subspecies and to produce hierarchical phenograms of these relationships (Figure 3). All three types of hierarchical clustering methods (centroid, UPGMA, and Ward's) produced similar phenograms that showed subspp. *georgiensis* and *maritima* clustering first when analyzing either character means from mature trees (Figure 3A) or from seedlings (Figure 3B). When using only data for mature trees, taxonomic distances for UPGMA clustering were 5.75 between *georgiensis* and *maritima*, 6.10 between *georgiensis* and *oklahomensis*, and 8.38 between *maritima* and *oklahomensis* (Figure 3A). Data from seedlings showed comparable distances of 5.22 between *georgiensis* and *maritima*, 6.48 between *georgiensis* and *oklahomensis*, and 7.14 between *maritima* and *oklahomensis* (Figure 3B). These two phenograms resulted from the same number of characters.
but indicated less taxonomic distance between subspecies for seedlings than for mature plants. Yet, when overlaid, the shapes of the two phenograms were almost identical.

For the next level of cluster analyses, all six of the sub-populations clustered within their subspecies (Figure 4), with Pennington Creek and Blue River sub-populations from Oklahoma the most similar in morphology and growth habit. The sub-populations of subsp. maritima, SW Delmarva and NW Delmarva, were more similar in morphology and habit than were the sub-populations of subsp. georgiensis (Drummond West and Drummond East) (Figure 4), even though the geographical distribution and separation between plants was much greater for subsp. maritima than for subsp. georgiensis (Figures 2B and 2C).

Cluster analyses also were performed on measurements of growth and morphology from individual OTUs of seedlings and mature plants. Again, the centroid, UPGMA, and Ward's clustering methods produced similar phenograms (not shown). With seedling data (22 characters, 27 OTUs), all three methods correctly placed the 10 OTUs from subsp. oklahomensis into one cluster, six out of 10 of the OTUs from subsp. maritima into another cluster, and placed all seven of the OTUs from subsp. georgiensis along with two from subsp. maritima into a third main cluster. The other two OTUs from subsp. maritima appeared as outliers. UPGMA analysis of 22 characters of mature plants (120 OTUs, 40 from each subspecies) also produced three main clusters (phenogram not shown) and correctly placed 37 of the 40 OTUs from subsp. oklahomensis into the first cluster. The second main cluster contained 32 of the 40 OTUs from subsp. georgiensis, one OTU from oklahomensis, and one from subsp. maritima. The third main cluster contained 30 of the 40 OTUs from subsp. maritima and three OTUs from subsp. georgiensis. The remaining OTUs from the three subspecies were placed in outlying clusters.
In the final cluster analysis, data from mature plants of the three subspecies and the species *Alnus japonica* (the outgroup) were used to produce an inferred phylogenetic tree by the neighbor-joining method (Figure 5). Based on 23 characters of morphology and growth habit, it was inferred that ancestors of subsp. *oklahomensis* were the first to diverge, followed by the divergence of the lines leading to subspp. *georgiensis* and *maritima* (Figure 5). The total Euclidean distances between subspecies were 4.35 between *oklahomensis* and *georgiensis*, 5.16 between *oklahomensis* and *maritima*, and 2.95 between *georgiensis* and *maritima*.

**Correlations Between Mature and Juvenile Characters**

Many characteristics of the subspecies were consistent between the 18-week-old seedlings and the mature trees. Correlation coefficients were \( r = 0.99 \) for leaf length, \( r = 0.92 \) for leaf length/width ratio, \( r = 0.99 \) for plant height, and \( r = 0.93 \) for stem or trunk dia. Correlation coefficients for other related characters were \( r = 1.00 \) for the correlation between health rating of mature trees and leaves per cm of seedlings, \( r = 0.99 \) for the shape of mature trees and the stem curvature of seedlings, \( r = 0.97 \) for leaf thickness of mature trees and leaf specific weight of seedlings, \( r = -0.99 \) for trunks per m\(^2\) of mature trees and stem thickness of seedlings, and \( r = 0.60 \) for canopy surface area of mature trees and total leaf surface area of seedlings.

**Edaphic and Climatic Characteristics**

Analysis of environmental characteristics of the three provenances revealed differences in both soil and climate (Table 3). Soil nitrate concentrations from the Georgia provenance were over twice those of the other two provenances, and soil phosphorus concentrations were different for all three areas (Table 3). Soil potassium, calcium, and magnesium concentrations from
Oklahoma samples were over twice those of the other two provenances. Soils from Oklahoma and Georgia were relatively high in organic matter (Table 3). Soils from Georgia and the Delmarva Peninsula had identical pH, while the pH of soils from Oklahoma was much greater (Table 3). Plants from Georgia were growing further above the water table than plants from the other two provenances, while plants on the Delmarva Peninsula (subsp. *maritima*) were growing closest to the water table. Plants from Georgia were in less shade than were plants of the other two subspecies, and the Georgia provenance received a greater amount of annual precipitation than did the other two areas (Table 3). The annual mean minimum and mid-winter minimum temperatures were lowest for the Delmarva provenance, while the annual mean maximum and mid-summer maximum temperatures were highest for the Oklahoma provenance (Table 3).

Analysis of covariance revealed some relationships between subspecies morphology/growth habit and local environmental conditions. Of the 206 potential relationships between environment and morphology/growth habit that were analyzed, 30 were significant at the $P \leq 0.05$ level (Table 4).

**DISCUSSION**

The most recent revision of the genus *Alnus* is a monograph by Furlow (1979) that is limited to those species found in the New World. Furlow's treatment was vigorous and contemporary, utilizing methods from numerical taxonomy and chemosystematics along with more traditional methods, and applying only three infrageneric ranks, the subgenus, the species, and the subspecies. The most important adjustment made by Furlow concerning the classification of *Alnus maritima* was to upgrade *Alnus* sect. *Clethropsis* (Murai 1964), which already contained *A. maritima* and two other closely related species, *Alnus nepalensis* D. Don
and *Alnus nitida* (Spach) Endl., to the rank of subgenus (Furlow 1979). It is curious that Furlow neglected to classify the two populations of *A. maritima* known at the time (those in Oklahoma and on the Delmarva Peninsula) as subspecies when his own working definition of a subspecies would have allowed him to do so. Furlow (1979) defined subspecies as "segments of species having relatively large geographic ranges and which are distinct in morphology and (to at least some degree) habitat. The category is used not only for those taxa showing distinct geographical distributions, but also for ecotypes" (Furlow 1979). Perhaps Furlow lacked the quantity of data needed to resolve the infraspecific variation that exists.

The Guide for Contributors to the Flora North America (Shetler et al. 1973) includes guidelines for the use of the infraspecific ranks of subspecies and variety that seem more objective than the definition used by Furlow (1979). We have used their guidelines dealing with morphology and phytogeography. Subspecies are either "geographically isolated populations that differ from one another by fewer characters than do species of the same genus and can be demonstrated to have some degree of interfertility," or subspecies are "ecologically specialized populations, particularly with respect to certain edaphic or climatic conditions, when there also is a morphological means of distinction" (Shetler et al. 1973). We have thoroughly examined the components found in these two definitions except for the degree of interfertility between the subspecies. In the case of *Alnus maritima*, the degree of interfertility is probably not a good indicator for infraspecific classification, because closely related species of *Alnus* hybridize readily in areas of sympatry, and many species of *Alnus* are extrinsically isolated, with distinct and isolated species, such as *Alnus glutinosa* (L.) Gartn. of western Europe and *Alnus rubra* Bong. of western North America, able to undergo successful artificial hybridization (Furlow 1979).
The fact that the three subspecies of *Alnus maritima* are so widely separated has removed many of the questions and problems associated with delimiting similar taxa that occur over a more continuous geographic distribution. The three subspecies of *A. maritima* undoubtedly are reproductively isolated. Along with absolute reproductive isolation, the three disjunct populations of *A. maritima* possess ample differences in morphology, growth habit (Tables 1 and 2), and habitat (Table 3) to warrant their classification as subspecies. Both the differences in character means (Tables 1 and 2) and the results of the cluster analyses (Figures 3, 4, 5 and analyses using individual OTUs) demonstrate that significant divergence has occurred between the three subspecies since the time of their geographic isolation. The fact that the sub-populations (Figure 4) and the individual OTUs clustered within their subspecies demonstrates the credibility and resolving power of the measured characters.

With this evidence at hand, one might question whether the three disjunct populations warrant classification as species rather than subspecies. Such a conclusion would be difficult to defend. With major similarities between the disjunct populations, including autumnal anthesis, production of both pistillate and staminate catkins during the same growing season as flowering, pistillate inflorescences (and later infructescences) solitary in leaf axils, and large strobili bearing fruit with reduced wings, characteristics not shared by any other American species of *Alnus*, the evidence leads us to conclude that the three populations are of the same species but worthy of separation at the infraspecific level.

Analysis of covariance showed relationships between some of the characters of mature plants in nature and the environmental conditions measured (Table 4). Of the 30 significant relationships, only a few are easily interpreted as possible causal relationships where an environmental factor, rather than genotype, may have been largely responsible for the variation
between specimens. As would be expected, canopy diameter and canopy surface area decreased with increasing percentage shade for all three subspecies (Table 4), illustrating the effects of competition with other trees, but shade/competition could not be the only factor responsible for the variation between subspecies. There was no statistical difference between subspp. *oklahomensis* and *maritima* for percentage shade (Table 3), yet subsp. *oklahomensis* had the greatest canopy dia. and canopy surface area, while subsp. *maritima* had the lowest measurements for these two characters (Table 1). All 30 of the significant relationships are similar to this example. Even with the effects of environment, ample phenotypic differences between subspecies are apparent. Still, some of the differences in habitat among the three provenances may have served as selective factors that influenced the timing and direction of genetic divergence of the three subspecies.

Subspecies *oklahomensis* is found growing in slightly to moderately alkaline soils, low in nitrate, very low in phosphorus, low in potassium, high in calcium, and high in magnesium (Table 3). Subspecies *oklahomensis* grows along fast-flowing streams and rivers in southern Oklahoma, where the summers are extremely hot and dry (Table 3). The greater root dry weights and greater root : shoot ratios of genotypes from Oklahoma (Table 2) may be an adaptation to some of these environmental conditions. Larger root systems may enable subsp. *oklahomensis* to obtain mineral nutrients from soils low in available nutrients (especially phosphorus), and/or the more extensive root systems may help secure plants and the soil around them in place along the turbulent waterways where they are found (Schrader and Graves 2000a). The Blue River and Pennington Creek flow so swiftly at many sites where plants are found that the river bottoms are stripped to the bedrock. At these sites, subsp. *oklahomensis* is found growing on the edge of the waterways, but also in small monotypic stands on islands. The only
islands that exist in these areas are those supporting *Alnus maritima*; all other soils are eroded. Canopies of subsp. *oklahomensis* growing on the edge of these waterways often extend out over the water as they compete for sunlight against taller trees growing farther from the water.

Subspecies *georgiensis* grows in a spring-fed swamp in slightly to moderately acidic soils that are low in phosphorus and very low in potassium (Table 3). The low concentration of potassium in soils of Drummond Swamp may have been partially responsible for the lower health rating seen in plants of subsp. *georgiensis* (Table 1). Potassium deficiency causes chlorosis and scorching of older leaves (Kozlowski and Pallardy 1997), symptoms we observed on some of the mature plants from Georgia. The greater annual precipitation in the Georgia provenance may be one reason why trees of subsp. *georgiensis* grow further above the water table than do trees from the other two subspecies (Table 3). The greater soil moisture provided by precipitation may help offset the need for trees in Georgia to be as closely associated with saturated soils as are the other two subspecies. Although the Georgia population covers a much smaller area than do the other two populations (Figure 2), it supports what is possibly the largest natural monotypic stand of *Alnus maritima* in the world. Pastureland at the northwest end of Drummond Swamp contains a grove of trees made up of hundreds of individuals covering approximately five hectares. This pasture has been under continuous grazing by cattle since at least 1943 (W. Nelson, pers. comm.), and the extreme herbivory appears to have provided a competitive advantage for subsp. *georgiensis* to establish and maintain such a large pure stand. Where it is found growing with other bottomland species, the overall large size (Table 1) and rapid growth (Table 2) of subsp. *georgiensis* make it very competitive with other tree species in Drummond Swamp.
Subspecies *maritima* is less conspicuous in its natural landscape than are the other two subspecies. Although all three subspecies grow as individuals in full sunlight, and in small monotypic stands, pure stands of this type are found relatively infrequently on the Delmarva Peninsula. The smaller, more shrub-like growth habit of subsp. *maritima* (Table 1) makes it less visually distinctive among other bottomland species, and it often is found as a member of the understory. The greater shade percentage and lower elevation above the water table recorded for subsp. *maritima* (Table 3), along with its relatively high health rating (Table 1), suggest that subsp. *maritima* has adapted to a slightly different niche than have the other two subspecies. Plants appear more shade tolerant and hydrophilic, qualities that make subsp. *maritima* well suited for the abundant, mature wetlands of the Delmarva Peninsula.

The peculiar disjunct distribution of the species *Alnus maritima* is a wondrous curiosity that is yet to be sufficiently explained. There has been much speculation about its origin. Some believe the population on the Delmarva Peninsula to be the oldest, and that the populations in Georgia and Oklahoma were established from Delmarva germplasm by Native Americans (Stibolt 1981) or some natural form of long-distance dispersal. While it is conceivable that geographic isolation could have allowed the speciation of *A. maritima* on the Delmarva Peninsula, the evidence does not support this. The other extant members of subg. *Clethropsis* (*Alnus nitida* and *Alnus nepalensis*), the only other autumn-blooming *Alnus* species, are indigenous only to southern Asia. Also important are the fossil remains of an intermediate taxon [*Alnus relatus* (Knowlton) Brown] that have been unearthed in Washington, Oregon, and Idaho; and the recognition of *A. maritima* and *Alnus japonica*, a species indigenous to Japan and eastern China, as living equivalents of *Alnus relatus* based on leaf morphology (Brown 1937, Chaney 1959, Chaney and Axelrod 1959, Graham 1965, Schrader and Graves 2000b). Even if we grant
the premise that *A. maritima* originated on or around the Delmarva Peninsula, the possibility of natural long-range dispersal to Oklahoma and Georgia seems very unlikely. Experimental results and observations with widely disjunct distributions indicate that long-distance dispersal is seldom the proper conclusion unless the species has seeds with impermeable seed coats and the disjuncts are taxonomically indistinguishable (Fryxell 1967, Löve 1967), a situation that is not true for *A. maritima*. Based on this evidence, Furlow's theory that ancestors of *A. maritima* migrated into North America via the Bering land bridge and spread across the United States before being forced into the present disjunct range (Furlow 1979) is much more plausible, and most new evidence supports this theory. It might be suggested that a species native only to warm areas of the United States (USDA hardiness zones 7a and 7b) could not have invaded North America via this extremely cold northern route. Yet, new data show that *A. maritima* from each subspecies can withstand mid-winter temperatures as low as -80°C (Schrader 2002), a level of hardiness similar to the most cold-resistant trees from subarctic regions (Vezina et al. 1997).

The most important summary to date of the divergence between the three subspecies of *Alnus maritima* is found in the Euclidean distances calculated from our measurements of morphology and growth habit. The inferred phylogenetic tree produced by PHYLIP software (Figure 5) supports Furlow's theory by estimating that the ancestral line to subsp. *oklahomensis* diverged first, followed by the divergence of the lines leading to the other two subspecies. Further evidence is the fact that the Euclidean distances between the subspecies (4.35 between *oklahomensis* and *georgiensis*, 5.16 between *oklahomensis* and *maritima*, and 2.95 between *georgiensis* and *maritima*) correspond well with the linear geographic distances between the three provenances (1100 km between Oklahoma and Georgia, 1930 km between Oklahoma and Delmarva, and 960 km between Georgia and Delmarva). Although still not entirely conclusive,
this new evidence supports Furlow's theory much better than it does the theory of long-distance dispersal.

To explain how *Alnus maritima* came to inhabit these three small, disjunct areas, we must consider more closely the ecology of this species. Starting with the more plausible theory that *A. maritima* once had a much more extensive distribution that has been gradually restricted (Furlow 1979), we can begin to use the evidence collected so far to explain the present-day distribution. Instead of asking why *A. maritima* inhabits only these three small provenances, we should ask why it continues to inhabit these areas. Species of *Alnus* have long been considered as pioneers in forest succession because they are fast-growing, nitrogen-fixing, actinorhizal plants (Newton et al. 1968, Benson and Sylvester 1993). *Alnus* has played a vital role in succession and soil development in deglaciated regions, both in the past (Heusser and Shackelton 1979) and present (Ugolini 1968). Palynological evidence indicates that *Alnus* was the dominant tree genus in North America and Europe during the postglacial period of the Early Holocene (10,000 to 8000 before the present) (Heusser and Shackelton 1979). On deglaciated sites, *Alnus* is normally the dominant tree genus from approximately year 20 to year 80 after glacial recession; then it is slowly replaced by larger, late-successional tree species (Newton et al. 1968, Ugolini 1968). By year 55 after glacial recession, the increasing nitrogen content in the forest floor reaches its peak, nitrogen fixation in *Alnus* roots is reduced due to the greater soil nitrogen concentrations, and soil conditions, improved greatly by the presence of *Alnus*, are now more suitable for other invading tree genera (Newton et al. 1968, Ugolini 1968). Finally, lack of shade tolerance causes *Alnus* to yield to the encroaching tree species once they exceed *Alnus* in height.

Most *Alnus* species grow well only in full sunlight (Furlow 1979) and are shade-intolerant (Franklin and Dymess 1973). *Alnus maritima* appears to be no exception. We
determined the average percentage shade for this species in extant populations (all 120 OTUs) to be only 25.5%. Its lack of shade tolerance, natural loss of early-successional advantage from nitrogen fixation in most environments, and climatic changes that eliminated the most important advantages of _A. maritima_ over other pioneer species may be the primary reasons for the extreme reduction in its distribution. With derived characters, such as corky, wingless fruits mainly dispersed by water, semi-shrub growth habit, autumn flowering, and reduced inflorescences, Furlow (1979) considers _A. maritima_ to be the most specialized of the New World _Alnus_ species. It is conceivable that many of the specialized characteristics of _A. maritima_ that make it the most hydrophilic of all American _Alnus_, may have given this species a strong advantage over other pioneer species under particularly wet conditions after glacial recession (Newton et al. 1968, Ugolini 1968). Later, the warmer, drier conditions of postglacial North America (Delcourt and Delcourt 1993) and the progression of late-successional tree species may have gradually forced _A. maritima_ into its present, meager distribution.

Why does _Alnus maritima_ continue to inhabit the three small provenances known at present? The reason that _A. maritima_ has survived may be that each of the three subspecies has evolved subtle tactics to compensate for its inherent lack of shade tolerance. Although all three subspecies have individuals found growing in full sunlight, the possible key to the survival of each of the subspecies is the behavior of plants that are not growing in full sunlight. In Oklahoma, plants on the riverbanks extend far over the water to capture available light. In Georgia, the plants are taller (Table 1) and better able to compete with the smaller bottomland tree species of the area. On the Delmarva Peninsula, at least some genotypes seem to have developed a greater degree of shade tolerance and tend to behave more like understory shrubs. Such adaptations, along with beneficial peculiarities in the local environments of each
provenance (islands in swift Oklahoma rivers, continuous cattle pastureland in Georgia,
abundant wetlands of the Delmarva Peninsula, etc.), may have allowed these populations to
survive.

Although our numerical analyses of morphology and growth habit segregated and defined
the subspecies, they also revealed diversity within each subspecies that may be unexpected in
populations inhabiting such a limited geographical range. The variation within subspecies is
revealed by the standard deviations for the characters of mature plants in nature (Table 1) and by
the clustering patterns of sub-populations (Figure 4) and individual OTUs. The standard
deviations were greatest for subsp. *oklahomensis* for most of the measures of tree size, but were
the lowest for subsp. *oklahomensis* for many of the leaf and shape measures (Table 1).
Conversely, subspp. *georgiensis* and *maritima* are evidently more diverse in leaf and shape
characteristics than is subsp. *oklahomensis*. Although not large enough to mask the
morphological differences between subspecies, the magnitudes of the standard deviations shown
in Table 1 suggest that enough genetic diversity may exist within the subspecies to allow them to
adapt to subtle changes in environment. Barring habitat destruction by humans or encroachment
by invasive species, it appears that even the small population of subsp. *georgiensis* may be
genetically fit for long-term survival within its natural range.

**TAXONOMIC TREATMENT**

The present work represents the first comprehensive treatment of *Alnus maritima* at the
infraspecific level. All known synonyms (legitimate and illegitimate) are included, along with
the description of each taxon and Latin diagnosis for each new taxon. A key to the three
subspecies and an illustration of diagnostic characters (Figure 6) are also included. Specimens
can be keyed to *A. maritima* by using the keys to North American *Alnus* provided in Furlow (1979) or Furlow (1997) and to subspecies by using the key provided here. In most cases, infraspecific identification will be greatly simplified by the extreme geographic separation between subspecies.

*Alnus maritima* (Marsh.) Muhl. ex Nutt.

*Alnus maritima* Muhl. ex Nutt., North American Sylva 1: 50. 1842. TYPE:


Large shrub or tree with a narrow to broad rounded crown, 3.5-8 (9.5) m in height; trunks usually several, erect, up to 9 (21) cm in diameter; bark brown when new, then turning light gray and becoming darker gray with age, smooth, becoming slightly rough with age; young stems light green becoming brown, with continuous solid pith, often with longitudinal ridges, slightly to moderately lustrous, slightly glaucous, sparsely to densely glandular, with sparse cylindrical trichomes; lenticels white, appearing after six months, 0.5-1 mm long, 1-2 mm wide, becoming obscured on stems after fourth or fifth year; leaf scars 0.5-2 mm long, 2-5 mm wide, bundle scars
inconspicuous. Buds gray to reddish-brown, ovoid to ellipsoid; stalk 0.5-1.5 mm long, 0.5-1 mm in diameter; body (2) 2.5-5 (6) mm long, (1) 2-2.5 (3) mm in diameter; scales 2, valvate, often resinous. Roots mainly fibrous, root:shoot ratio of ca. 0.40-0.52 for seedlings. Leaves simple, dark green to very dark green above, paler green below; ovate, elliptic or narrowly elliptic, or obovate; blade (5) 6.5-8.5 (10) cm long, (2.9) 3.3-4.7 (6.5) cm wide; surfaces glabrous, resinous, sparse cylindrical trichomes on primary and secondary veins; adaxial surface dull to lustrous, slightly to moderately glandular; abaxial surface dull, slightly to moderately glandular; venation pinnate, simple craspedodromous, with (6) 6-10 (11) secondary veins on each side of midrib; primary veins straight and moderate to stout (ca. 2.0-2.5% of leaf width); secondary veins with uniform, moderately acute angle of divergence, moderately thick, uniformly curved, sometimes branching once, ending in teeth at the margin; tertiary veins with acute-right, sometimes right-right (exmedial-admedial) angle of origin, random reticulate anastomoses, simple and forked percurrent; quaternary veins orthogonal; apex acute to obtuse, sometimes acuminate; margin serrate with single ascending teeth, each enlarged at the tip into a single gland; base cuneate; petiole (10) 14-20.5 (24) mm long, (0.6) 0.9-1.5 (2) mm in diameter, glabrous, moderately glandular. Staminate inflorescences 2-6 catkins in racemose clusters at ends of current year's twigs, produced in midsummer of current growing season; at anthesis (mid-August to mid-September of same season), yellow and pendent, 2-8 cm long, 5-7 mm in diameter, on peduncles 4-18 mm long 0.5-1 mm in diameter, deciduous. Pistillate inflorescences solitary in axils of the first to fourth leaves from apex, on twigs bearing staminate catkins, produced in midsummer of current growing season, at anthesis (mid-August to mid-September of same season), erect, ovate to elliptic, (2) 3-5 (6) mm long, (1) 1.5-3 (3.5) mm in diameter, on peduncles (3) 4-7 (8) mm long, 1-2 mm in diameter. Infructescences, ovoid to broadly ovoid,
ellipsoid to broadly ellipsoid, or obovoid to broadly obovoid strobili (11.4) 16-21 (25) mm long, (9.2) 12.5-15 (18) mm in diameter, on peduncles 5-10 mm long, 1-2 mm in diameter, maturing one year after pollination. Fruits light to dark brown, elliptic, 2-4 mm long, 2-3 mm wide, with wings narrow to absent and 2 persistent styles 0.5-1 mm long.

Large riparian shrub or tree, that grows from near sea level to about 300 m in elevation; in, or on the edge of, ponds, streams, or rivers; usually in full sunlight. Occurs naturally in south-central Oklahoma, northwestern Georgia, and Maryland and Delaware on the Delmarva Peninsula.

Key to subspecies of *Alnus maritima*

A. Leaves ovate, elliptic, or narrowly elliptic, only rarely obovate, length:width ratio > 2.1, apex acute sometimes acuminate, never obtuse; strobili length:width ratio > 1.5; large shrub or small tree with broad rounded crown, as wide as or slightly wider than it is tall; southern Oklahoma ..................................................... 2. *A. maritima* subsp. *oklahomensis*

A. Leaves obovate to elliptic, length:width ratio ≤ 2.1, apex acute to obtuse, sometimes acuminate; strobili length:width ratio ≤ 1.5; shrubs or trees taller than they are wide; eastern United States.

B. Strobili ovoid to broadly ovoid, ellipsoid to broadly ellipsoid, never obovoid, ≥ 19 mm long at maturity, length:width ratio ≥ 1.3; leaf length:width ratio < 1.8; medium to large shrub with a narrow to broad rounded crown, 3.5-6 (7.5) m in height; the Delmarva Peninsula .......................... 1. *A. maritima* subsp. *maritima*

B. Strobili ovoid to broadly ovoid, ellipsoid to broadly ellipsoid, or obovoid to broadly
1. *Alnus maritima* subsp. *maritima*.

Medium to large shrub with a narrow to broad rounded crown, 3.5-6 (7.5) m in height; trunks erect, up to 5.5 (8.3) cm in diameter. Buds gray to reddish-brown, obovoid to elipsoid; stalk 0.5-1.5 mm long, 0.5-1 mm in diameter; body (2) 3-5 (6) mm long, (1.5) 2-2.5 (3) mm in diameter; scales 2, valvate, often resinous. Roots mainly fibrous, root:shoot ratio of ca. 0.42 for seedlings. Leaves obovate to elliptic; blade (5) 6-8.5 (9.5) cm long, (3) 3.5-5 (5.6) cm wide; abaxial surface dull, moderately glandular and uniform over surface; venation pinnate, simple craspedodromous, with (6) 6-9 (10) secondary veins on each side of midrib; primary veins straight and moderate to stout (ca. 2.2% of leaf width); apex acute to obtuse, sometimes acuminate; petiole (10) 15-20 (23) mm long, (0.8) 1-1.5 (2) mm in diameter. Pistillate inflorescences ovate to elliptic, (2) 3-5 (6) mm long, (1.5) 2-3 (3.5) mm in diameter, on peduncles (3) 3.5-7 (8) mm long, 1-2 mm in diameter. Infuctescences ovoid to broadly ovoid, or ellipsoid to broadly ellipsoid strobili (15.2) 18.5-22 (25) mm long, (12.8) 13.5-15.5 (16) mm in diameter, on peduncles 5-10 mm long, 1-2 mm in diameter, maturing one year after pollination.

Large riparian shrub, that grows at or near sea level, in or on the edge of ponds or slow flowing rivers, some of which are slightly brackish and below the mean high-tide line; in full sunlight or among other bottomland trees and shrubs, where it behaves much like an understory
plant. Facultative acidophyte growing in wet, acidic soils that are low in phosphorus and very low in potassium. This subspecies occurs naturally in four counties (Caroline, Dorchester, Wicomico, and Worcester) in Maryland and two counties (Kent and Sussex) in Delaware, on the Delmarva Peninsula. Compared to the other subspecies, subsp. *maritima* is smaller for every measure of overall plant size for both mature trees and seedlings, with a canopy shape that is normally taller than it is wide, but with a canopy surface area about half that of the other two subspecies; it is more shrub-like, with smaller trunks (2.5-5.5 cm in diameter) and more trunks per m² of canopy (ca. 1.75); leaves have a lower length:width ratio (ca. 1.76); strobili never appear obovoid, and have a length:width ratio (ca. 1.38) midway between that of the other two subspecies; seedlings have smaller stems and grow more slowly, accumulating dry weight more slowly than the other two subspecies; plants appear to be more hydrophylic, with about 60% of the plants growing with roots completely submerged in water.

**COMMON NAMES:** Seaside alder, brook alder, Delmarva alder.

**REPRESENTATIVE SPECIMENS:** U.S.A., **MARYLAND.** **Worcester Co.:** 2.5 miles (4.0 km) W of Snow Hill, Schrader (S.) 81 (OKL), 82 (GA), 83 (MARY), 84 (NCU). **Wicomico Co.:** E side of Salisbury, N side of Shumaker Pond, S. 85 (ISC), 86 (US), 87 (A). **Dorchester Co.:** 0.5 miles (0.8 km) NW of Sharptown, NW side of Nanticoke River, S. 90 (MU), 91 (NY), 92 (UC), 93 (WIS); 2.5 miles (4.0 km) E of Hurlock, E side of Marshyhope Creek, S. 94 (OKLA), 95 (F), 96 (KANU), 97 (UARK). **DELAWARE.** **Sussex Co.:** S side of Bethel, on the S side of Broad Creek, S. 88 (NA), 89 (MO); SW of Milford, N side of Abbott's Pond, S. 98 (MICH), 99 (DOV), 100 (CAS), 101 (BH); 5 miles (8.1 km) S of Milford, W end of Hudson's Pond, S. 102 (TEX), 103 (STAR), 104 (RSA), 105 (FLAS); Just S of Angola, SE side of Burton Pond, S. 106 (OS), 107 (MSC), 108 (DUR), 109 (KSC), 110 (NLU); NW side of Millsboro, NE
side of Betts Pond, S. 111 (MASS), 112 (UMO), 113 (USCH); 2 miles (3.2 km) W of Millsboro, E end of Ingram Pond, S. 114 (OSC), 115 (CM); E side of Concord, N side of Concord Pond, S. 116 (LTU), 117 (BRIT), 118 (OSH), 119 (TAMU), 120 (K).

2. *Alnus maritima* subsp. *oklahomensis* Schrader & Graves, subsp. nov.


Haec subspecies restricta ad Oklahoma meridionalem. Differt a ceteris subspeciebus forma lata fruticosa vel arborea, altitudine minori quam latitudine; foliis anguste ellipticis, ellipticis, vel ovatis, 2.1-2.6plo longioribus quam latitis; et strobilis 1.5-1.75plo longioribus quam latitis.

Large shrub or small tree with a broad-rounded crown, 3.5-7 (9.5) m in height; trunks erect, up to 12 (21) cm in diameter. Buds gray to reddish-brown, obovoid to elipsoid; stalk 0.5-1.5 mm long, 0.5-1 mm in diameter; body (2) 2.5-4 (5) mm long, (1) 2-2.5 (3) mm in diameter; scales 2, valvate, often resinous. Roots mainly fibrous, root:shoot ratio of ca. 0.52 for seedlings. Leaves ovate, elliptic, or narrowly elliptic, only rarely obovate; blade (6.8) 7.5-9 (10) cm long, (2.9) 3-4 (4.6) cm wide; abaxial surface dull, slightly glandular, more densely glandular on and
near primary and secondary veins; venation pinnate, simple craspedodromous, with (6) 7-10 (11) secondary veins on each side of midrib; primary veins straight and stout (ca. 2.5% of leaf width); apex acute, sometimes acuminate; petiole (10) 13-21 (23) mm long, (0.6) 0.75-1.5 (2) mm in diameter. Pistillate inflorescences ovate to elliptic, (2) 3-4.5 (5) mm long, (1) 1.5-2.5 (3) mm in diameter, on peduncles (4) 5-7 (8) mm long, 1-2 mm in diameter. Infructescences ovoid, ellipsoid, or obovoid strobili (11.4) 16-22 (25) mm long, (9.2) 11-14 (16) mm in diameter, on peduncles 5-10 mm long, 1-2 mm in diameter, maturing one year after pollination.

Riparian shrub or tree, found growing in full sunlight on islands within fast-flowing rivers and streams; or on the edge of waterways, under the edge of the forest canopy, with direct sunlight much of the day. Facultative basiphyte / calciphyte, growing in wet, alkaline, sandy to rocky soils, low in nitrate, very low in phosphorus, low in potassium, high in calcium, and high in magnesium. This subspecies occurs naturally in only two counties (Johnston and Pontotoc) in south-central Oklahoma where it grows in and along rivers and streams of the Red River watershed. Subspecies oklahomensis is the most distinct of the three subspecies. Compared to the other subspecies, subsp. oklahomensis forms a broader crown, with a normal canopy shape that is slightly wider than it is tall, and fewer trunks per m² of canopy (ca. 0.81); leaves are longer (ca. 8.62 cm) and narrower (ca. 3.63), with a greater length:width ratio (ca. 2.3), and are more elliptic, often ovate; strobili are narrower, with a greater length:width ratio (ca. 1.56); seedlings are more densely foliated and have a greater root:shoot ratio (ca. 0.52).

**COMMON NAMES:** Seaside alder, Oklahoma alder.

**REPRESENTATIVE SPECIMENS:** U.S.A., OKLAHOMA. Johnston Co.: Just N of Connerville, small sandy island in Blue River, Schrader (S.) 1 (GA), 2 (MARY); 1.5 miles (2.42 km) N of Reagan, N bank of Pennington Creek, S. 3 (DOV), 4 (NCU), 5 (MU); 6.0 miles (9.7
km) NW of Tishomingo, S bank of Pennington Creek, S. 6 (NY), 7 (UC), 8 (WIS), 9 (OKLA), 10 (F); 6.5 miles (10.5 km) NW of Tishomingo, N bank of Reagan Branch Creek, S. 11 (KANU), 12 (UARK); 4.0 miles (6.44 km) NW of Tishomingo, Pennington Creek at Slippery Falls, S. 13 (MICH), 14 (CAS), 15 (BH); 1 mile (1.61 km) N of Tishomingo, W bank of Pennington Creek, S. 16 (TEX), 17 (OKL), 18 (STAR); 1.3 miles (2.09 km) N of Tishomingo, W bank of Cedar Creek, S. 19 (RSA), 20 (FLAS); 7.0 miles (11.26 km) NE of Tishomingo, SW side of Blue River, S. 21 (OS), 22 (MSC); 7.0 miles (11.26 km) NE of Tishomingo, island in Blue River, S. 23 (DUR), 24 (KSC); 7.5 miles (12.07 km) NE of Tishomingo, W bank of Blue River next to cement bridge, S. 25 (A, ISC, MO, NA, OKL, US), 26 (NLU), 27 (MASS); 7.5 miles (12.07 km) NE of Tishomingo, E bank of Blue River just N of cement bridge, S. 28 (UMO), 29 (USCH); 8.0 miles (12.87 km) NE of Tishomingo, W bank of Blue River, S. 30 (OSC), 31 (CM), 32 (LTU), 33 (BRIT); 9.5 miles (15.29 km) NE of Tishomingo, E bank of Blue River, S. 34 (OSH), 35 (TAMU); 10 miles (16.09 km) NE of Tishomingo, E bank of Blue River, S. 36 (K), 37 (ISC); 10 miles (16.09 km) NE of Tishomingo, island toward the E side of Blue River, S. 38 (ISC), 39 (ISC); 1 mile (1.61 km) S of Pontotoc, N side of a spring fed tributary of Little Blue River, S. 40 (ISC).

3. *Alnus maritima* subsp. *georgiensis* Schrader & Graves, subsp. nov.


Haec subspecies restricta ad Georgia boreo-occidentalem. Differt a ceteris subspeciebus forma alta angusta fruticosa vel arborea, altitudine 1.5-2plo majori quam latitudine; foliis
Narrow-crowned large shrub or tree 5.5-8 (9.5) m in height; trunks erect, up to 9 (13) cm in diameter. Buds gray to reddish-brown, obovoid to ellipsoid; stalk 0.5-1.5 mm long, 0.5-1 mm in diameter; body (2) 3-4.5 (5) mm long, (1.5) 2-2.5 (3) mm in diameter; scales 2, valvate, often resinous. Roots mainly fibrous, root:shoot ratio of ca. 0.41 for seedlings. Leaves obovate to elliptic; blade (5.7) 6.5-8.5 (10) cm long, (3) 3.5-5 (6.5) cm wide; abaxial surface dull, moderately glandular and uniform over surface; venation pinnate, simple craspedodromous, with (6) 7-9 (10) secondary veins on each side of midrib; primary veins straight and moderate to stout (ca. 2.0% of leaf width); petiole (10) 14-21 (24) mm long, (0.8) 1-1.5 (2) mm in diameter. Pistillate inflorescences ovate to elliptic, (2) 3-4.5 (5.5) mm long, (1.5) 2-3 (3.5) mm in diameter, on peduncles (3) 4-6.5 (8) mm long, 1-2 mm in diameter. Infructescences ovoid to broadly ovoid, ellipsoid to broadly ellipsoid, or obovoid to broadly obovoid strobili (14) 14.5-19 (24) mm long, (11.4) 12.5-15.5 (18) mm in diameter, on peduncles 5-10 mm long, 1-2 mm in diameter, maturing one year after pollination.

Riparian large shrub or tree, that grows in full sunlight, in open water and on bog mats in the middle of a swamp, and on pasturelands adjacent to the swamp; or among other bottomland trees as a competitive member of the forest canopy. Facultative acidophyte growing in wet, acidic soils that are low in phosphorus and very low in potassium. This subspecies occurs naturally in one county (Bartow) in northwestern Georgia, where it grows in and around one 50-hectare swamp (Drummond Swamp). Compared to the other subspecies, subsp. georgiensis grows taller and has a narrower crown, with a canopy shape that is often one-and-one-half to two times taller than it is wide; leaves are thicker and have a length:width ratio (ca. 1.86) midway
between those of the other two subspecies; strobili are shorter (ca. 17.3 mm), with a lower length:width ratio (ca. 1.24); seedlings are taller, are sparsely foliated, and have leaves of greater specific weight.

**COMMON NAMES:** Seaside alder, Georgia alder.

**REPRESENTATIVE SPECIMENS:** U.S.A., **GEORGIA. Bartow Co.:** 0.5 miles (0.81 km) SW of Euharlee, S side of creek that drains Drummond Swamp, at the E end of the swamp, Schrader (S.) 41 (OKL), 42 (MARY), 43 (DOV), 44 (NCU), 45 (MU), 46 (NY), 47 (UC), 48 (WIS), 49 (A, GA, ISC, MO, NA, US), 50 (OKLA), 51 (F), 52 (KANU), 53 (UARK); 0.5 miles (0.81 km) SW of Euharlee, SE end of Drummond Swamp, S. 54 (MICH), 55 (CAS); 0.5 miles (0.81 km) SW of Euharlee, NW end of Drummond Swamp, 20 m E of Bill Nelson Rd., S. 56 (BH), 57 (TEX), 58 (GA), 59 (STAR), 60 (RSA); 0.5 miles (0.81 km) SW of Euharlee, NW end of Drummond Swamp, 30 m E of Bill Nelson Rd., S. 61 (FLAS), 62 (OS), 63 (MSC), 64 (DUR), 65 (KSC); 0.5 miles (0.81 km) SW of Euharlee, NW end of Drummond Swamp, 35 m E of Bill Nelson Rd., S. 66 (NLU), 67 (MASS), 68 (UMO), 69 (USCH), 70 (OSC); 0.5 miles (0.81 km) SW of Euharlee, NW end of Drummond Swamp, 40 m E of Bill Nelson Rd., S. 71 (CM), 72 (LTU), 73 (BRIT), 74 (OSH), 75 (TAMU); 0.5 miles (0.81 km) SW of Euharlee, NW end of Drummond Swamp, 50 m E of Bill Nelson Rd., S. 76 (K), 77 (ISC), 78 (ISC), 79 (ISC), 80 (ISC).

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LITERATURE CITED


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Figure Captions

Figure 1. Location of the three disjunct populations (subspecies) of *Alnus maritima* found in south-central Oklahoma, northwestern Georgia, and on the Delmarva Peninsula (eastern Maryland and southern Delaware). Distances between these natural populations are 1100 km for the Oklahoma and Georgia populations, 1930 km for the Oklahoma and Delmarva populations, and 960 km between the populations in Georgia and on the Delmarva Peninsula.

Figure 2. Native ranges of the three subspecies of *Alnus maritima*. Known distributions are shown surrounded by dark, heavy lines (—). Locations of OTUs for this study are shown by symbols (•).  
B. Distribution of *Alnus maritima* subsp. *maritima* found in Maryland and Delaware on the Delmarva Peninsula. The dashed line (······) divides the Chesapeake Bay watershed from the Delaware Bay watershed (SW Delmarva sub-population from NE Delmarva sub-population). 
C. Distribution of *Alnus maritima* subsp. *georgiensis* found in Drummond Swamp, Bartow County, Georgia.

Figure 3. UPGMA clustering of the three subspecies of *Alnus maritima* based on 22 characters of morphology and growth habit of mature trees found in nature (A) and based on 22 characters of morphology, growth habit, and developmental rate of 18-week-old seedlings (B). The scale represents the taxonomic distance measured along the horizontal lines.
Figure 4. UPGMA clustering of sub-populations of *Alnus maritima* based on 22 characters of morphology and growth habit of mature trees found in nature. The scale represents the taxonomic distance measured along the horizontal lines. Pennington Creek and Blue River are sub-populations of subsp. *oklahomensis*, Drummond West and Drummond East are sub-populations of subsp. *georgiensis*, and the two main sub-populations of subsp. *maritima* are SW Delmarva and NE Delmarva. See text for details.

Figure 5. Inferred phylogenetic relationship between the three subspecies of *Alnus maritima* based on 23 characters of morphology and growth habit of mature plants. *Alnus japonica*, an Asian species from the primitive subg. *Alnus* (Furlow 1979), was designated as the outgroup. Numbers indicate the branch lengths from a point of divergence to the position of an extant taxon or the distance between successive points of divergence (A to B). The number next to *Alnus japonica* represents the distance from *A. japonica* to "A," the first point of divergence. The total Euclidean distances between subspecies were 4.35 for *oklahomensis* to *georgiensis*, 5.16 for *oklahomensis* to *maritima*, and 2.95 for *georgiensis* to *maritima*.

Figure 6. Diagnostic characters of the three subspecies of *Alnus maritima*: subsp. *oklahomensis* (left), subsp. *georgiensis* (middle), and subsp. *maritima* (right). A. mature leaves (actual size). B. mature infructescences (actual size). C. growth habits (size and shape) of mature trees (note scale bar).
Figure 1.
Figure 3.

Figure 4.
Figure 5.
Figure 6.