Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska

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MECHANISMS OF PRIMARY SUCCESSION FOLLOWING DEGLACIATION AT GLACIER BAY, ALASKA[1]

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Abstract. In primary succession following deglaciation at Glacier Bay, Alaska, we tested the hypothesis that the major effect of initial nitrogen-fixing colonizers is to facilitate establishment of late-successional dominants and that other possible causes of successional change (e.g., life history factors governing seed rain and competitive interactions among species) need not be invoked. Environment changed dramatically through the first 200 yr of succession. Soil organic matter increased 10-fold in the upper mineral soil with corresponding increases in soil moisture, total nitrogen (N), and capacity to support plant growth and declines in bulk density, pH, and total phosphorus (P). Plant growth in pioneer soils tended to be simultaneously limited by both N and P, as well as by unknown factors (perhaps lack of mycorrhizae), whereas only P limited growth in older soils. Light availability to seedlings declined through succession.

Early-successional species (*Epilobium latifolium, Dryas drummondii*) had smaller seeds, younger age at first reproduction, shorter life-span, and shorter height at maturity than did mid-successional (alder, *Alnus sinuata*) and late-successional species (sitka spruce, *Picea sitchensis*). Seed rain of alder and spruce was negligible in the pioneer stage, increased prior to the stage in which a species was dominant, and was greatest in the stage in which a species dominated. Vegetation in each successional stage inhibited germination and initial establishment of sown alder and spruce seeds (except a tendency of the "black-crust" algal/microbial community in the pioneer stage to enhance survivorship). Removal of the surface litter layer generally enhanced germination and survivorship, particularly of alder. Comparisons of germination in the greenhouse and the field indicated that climatic or indirect vegetation effects (e.g., differential seed predation) and allelopathy also reduced germination and establishment in vegetated communities.

Naturally occurring spruce seedlings grew most rapidly in the *Dryas* and alder stages and most slowly in the spruce stage. Similarly, growth of spruce seedlings transplanted into each successional stage was facilitated by the *Dryas* (nonsignificantly) and alder stages but inhibited by the spruce stage, relative to earlier successional stages. Facilitation of growth of natural and transplanted spruce seedlings by *Dryas* and alder stages was associated with higher N and P uptake and tissue nutrient concentrations, whereas nutrient uptake and concentration in spruce seedlings declined in the spruce stage. By contrast, transplanted alder seedlings grew rapidly and accumulated most nutrients in the pioneer stage and were strongly inhibited by subsequent stages.

The facilitative effect of *Dryas* and alder comes primarily from inputs of organic matter and associated N. Addition of alder litter stimulated nutrient uptake and growth of transplanted spruce seedlings in the pioneer and *Dryas* stages, whereas shading had no effect on growth of spruce seedlings. Root trenching and planting of spruce near isolated alders indicated that, although the net effect of alder is facilitative, alder also inhibits growth of spruce seedlings through competition for soil resources. Strong root competition also occurs in the spruce stage. Alder competitively inhibits *Dryas*, primarily by shading but also through the physical and allelopathic effects of its litter.

In general, both at Glacier Bay and elsewhere, life history traits determine the pattern of succession. Changes in competitive balance accompanying successional changes in environment provide the mechanism for changes in species dominance. Initial site conditions (and facilitation, where present) influence the rate of change and final state of community composition and productivity. We conclude that no single factor or mechanism fully accounts for primary succession at Glacier Bay.

Key words: alder; competition; Dryas; *facilitation; germination; growth; Glacier Bay; nitrogen; phosphorus; spruce; succession.*

INTRODUCTION

Facilitation is the process by which colonizing species improve the environment for later successional species and, in the process, place themselves at a competitive disadvantage. On the basis of observations rather than experimentation, facilitation was long presumed to be a major mechanism causing ecological succession (Clements 1916, Tansley 1920). This paradigm has been questioned (Drury and Nisbet 1973, Connell and Slatyer 1977) because experimental studies generally demonstrate that early-successional species inhibit rather than facilitate the growth of later species (Keever 1950, Niering and Goodwin 1974, Harcombe 1977, Sousa 1979, Van Hulst 1979, Hils and Vankat 1982, Armesto and Pickett 1986, Walker and Chapin 1986). However, most of these studies were conducted in old fields or relatively high-resource environments, where soils are well developed, and facilitation is least likely to be important (Connell and Slatyer 1977, Vitousek and Walker 1987, Walker and Chapin 1987).

Facilitation is presumed to be the major successional mechanism in severe environments, where colonizing plants augment the availability of resources to a level required by later successional species (Connell and Slatyer 1977, Tilman 1982, 1985). Low nutrient levels (Viereck 1966, Van Cleve et al. 1971, Johnson et al. 1976, Robertson and Vitousek 1981, Vitousek et al. 1987, Walker 1989) and nutrient limitation to plant growth (Schoenike 1958, Lawrence et al. 1967, Walker and Chapin 1986, Wood and del Moral 1987, del Moral and Wood 1993) have been implicated as factors limiting colonization in early primary succession. Symbiotic N-fixers are often prominent in early primary succession (Lawrence et al. 1967, Stevens and Walker 1970, Walker and Syers 1976, Gorham et al. 1979, Blundon and Dale 1990) and can directly enhance growth of associated species in primary succession (Lawrence 1951, 1958, Schoenike 1958, Lawrence et al. 1967, Gadgil 1971, Dancer et al. 1977, Bradshaw 1983, Binkley et al. 1984, Richardson and Evans 1986, Morris and Wood 1989, del Moral and Wood 1993) and in secondary succession (Tarrant and Trappe 1971, Uemura 1971, Binkley 1992). In other cases, the rapid growth of woody N-fixers in primary (Walker and Chapin 1986) or secondary succession (Binkley 1992, Shainsky and Radosevich 1992) leads to dense stands that dominate resources and inhibit colonization or growth of later successional species (Walker 1993).

Primary succession is unlikely to be a simple consequence of any single process (e.g., facilitation by N-fixing colonists) or species trait (e.g., shade tolerance; Quinn and Dunham 1983, Huston and Smith 1987, Pickett et al. 1987b, Walker and Chapin 1987, Burrows 1990, Matthews 1992, del Moral and Wood 1993). Recent studies have examined multiple factors and processes governing succession (Sousa 1979, Walker

and Chapin 1987, Burrows 1990, De Steven 1991, Farrell 1991, Gill and Marks 1991, del Moral and Wood 1993), but none of these has demonstrated facilitation to be the major mechanism responsible for successional change. In order to evaluate the possible importance of facilitation we studied one of the classic examples of facilitation, succession following deglaciation at Glacier Bay, Alaska, where early establishment by N-fixing *Dryas drummondii* Richards. and alder [*Alnus sinuata* (Reg.) Rydb.] is closely associated with accumulation of soil N (Crocker and Major 1955, Ugolini 1968, Bormann and Sidle 1990) and a change in dominance to spruce [*Picea sitchensis* (Bong.) Carr.; Cooper 1923b, 1939, Lawrence et al. 1967, Reiners et al. 1971]. Here we tested the hypotheses that: (1) the presence of initial N-fixing colonizers (*Dryas* and alder) facilitates the establishment of spruce, and (2) other possible causes of succession (e.g., life history factors governing seed rain and competitive interactions among species) are of minor importance in primary succession at Glacier Bay.

STUDY SITE

Glacier Bay in southeastern Alaska (59° N, 136° W) is a Y-shaped fjord over 100 km long, whose lowlands were covered by glacial ice until ≈230 yr ago (Cooper 1923a, 1937). The subsequent rapid glacial retreat, averaging 0.4 km/yr (Goldthwait 1966), which is 15-fold more rapid than that of any other tidewater glacier (Lawrence 1958), exposed extensive areas of glacial till to plant colonization. Locations of glacial termini have been recorded frequently during glacial retreat (e.g., Vancouver 1798, Reid 1892, Cooper 1923a, 1937, Field 1947, McKenzie and Goldthwait 1971), making it possible to date precisely the deglaciation of specific sites (Fig. 1). Glacial till along the east arm of Glacier Bay is derived from metamorphosed sandstone, limestone, and igneous intrusions (Cooper 1923a, Brew et al. 1978) and has been extensively homogenized during early and late neoglacial advances (Haselton 1966). Soils in the pioneer stage have high pH, low organic content, high bulk density, and low cation exchange capacity, parameters that change substantially through succession (Crocker and Major 1955, Ugolini 1966, 1968).

The climate of Glacier Bay is oceanic, with a mean annual temperature of 5°C (January −3°, July 13°C) and annual precipitation of 1400 mm (Crocker and Major 1955, Loewe 1966, Streveler and Paige 1971). Summer temperatures average 3°C cooler in the upper bay than at the mouth (Cooper 1923b, Sharman 1987).

Previous research has documented four major successional stages along the east arm of Glacier Bay (Cooper 1923b, 1931, 1939, Lawrence 1958, Decker 1966, Reiners et al. 1971). During the first 20 yr after glacial retreat, till is gradually colonized by a pioneer community consisting of a "black crust" of blue-green algae, gametophytes of *Equisetum variegatum*, lichens, and liverworts (Worley 1973, Lawrence 1979), with
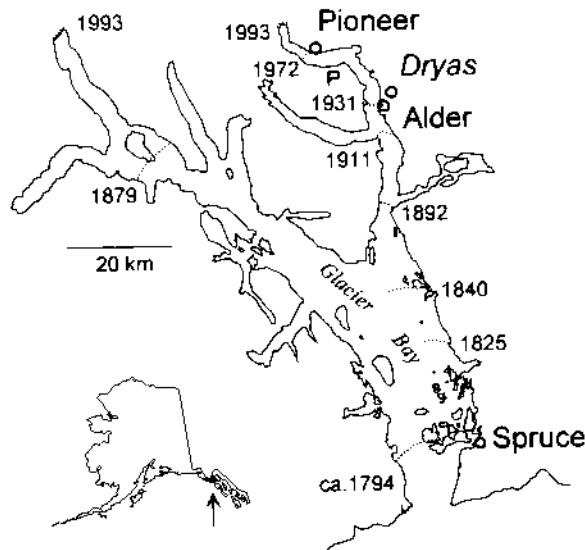
FIG. 1. Location of study sites in four successional stages (pioneer, *Dryas*, alder, and spruce) at Glacier Bay, Alaska, with historically documented and dendrochronologically inferred locations of glacier termini. Location of a second pioneer site (P) with scattered alders is also indicated. Inset shows the location of Glacier Bay National Park and Preserve (GBNPP) in southeastern Alaska (arrow).

alder stage at Nunatak Cove (previously called Anchorage Cove) from 1929 to 1940. Tree cores (C. L. Fastie, *unpublished data*) and ships' records (Vancouver 1798, Cooper 1923*b*) indicated that our spruce stage south of the Bartlett River on the terminal moraine of the most recent glacial advance (Goldthwait 1966) became ice free ≈1760–1775.

Our pioneer stage had <5% vascular plant cover in 1986, when our study began (Fig. 2). Our *Dryas* stage (Fig. 3) was studied by Ugolini (1968) and Decker (1966) when it was similar to our present pioneer stage and by Reiners et al. (1971: their sites 2 and 3) when *Dryas* began to invade. Our alder stage (Fig. 4) had been studied by Cooper (1931: his site 45, his Fig. 14) when it was in the pioneer stage, by Crocker and Major (1955: their photograph 1), Lawrence (1951, 1958: his photograph 14D), Schoenike (1958), and Lawrence et al. (1967: their photograph 1), when it was largely dominated by *Dryas*, and by Reiners et al. (1971: their site 4) when it was a young alder thicket. Our spruce stage (Fig. 5) had been studied previously as a spruce forest by Cooper (1939: his site 58), Crocker and Major (1955), Ugolini (1968), and Reiners et al. (1971: their site 6).

scattered forbs (particularly *Epilobium latifolium* L.), *Dryas drummondii* (a mat-forming dwarf shrub that fixes N; Lawrence et al. 1967), willows (*Salix* spp.), cottonwood (*Populus trichocarpa* Torr. and Gray), and spruce. From this initial pioneer stage, there is a gradual transition to a *Dryas* stage after ≈30 yr, where the ground surface is covered by a continuous mat of *Dryas* with persistent individuals of willow, cottonwood, alder, and spruce. About 50 yr after deglaciation, alder increases in abundance to form dense thickets, and *Dryas* disappears. After ≈100 yr, spruce overtops alder. After thousands of years, the spruce forest may change to a *Sphagnum*-dominated muskeg (Lawrence 1958, Ugolini and Mann 1979, Noble et al. 1984), but this stage is beyond the 230-yr time frame of the most recent glacial retreat at Glacier Bay and is omitted from the present study. Detailed descriptions of these successional stages and intermediate phases are provided by Cooper (1923*b*, 1931, 1939), Lawrence (1958), Decker (1966), Reiners et al. (1971), and Noble et al. (1984).

With the help of the National Park Service, we located four general areas, each ≈2 km², that are the largest areas in Glacier Bay of the four successional stages described above (Fig. 1). Historical photographs archived at Glacier Bay National Park and Preserve (Gustavus, Alaska) indicate that our pioneer stage on the north shore of Muir Inlet became ice free from 1975 to 1980 (near W. O. Field photo stations 39 and 40), the *Dryas* stage along upper Nunatak Creek east of Nunatak Knob (former position of the McBride Remnant) from 1950 to 1960 (Haselton 1966), and the
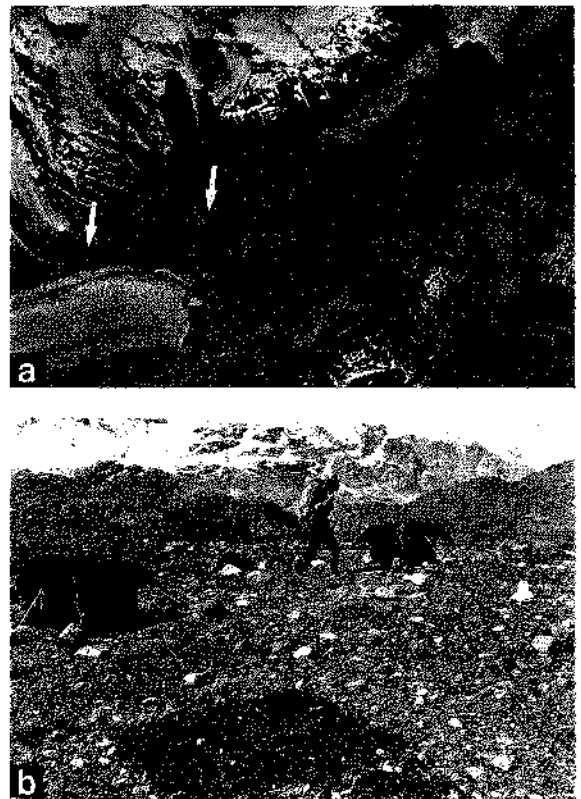

FIG. 2. Aerial view of pioneer stage (a) at the time of deglaciation in 1974 (courtesy of GBNPP; arrows indicate borders of the study area ≈2 km apart) and (b) at the beginning of the study in 1987. A shade frame for the seedling experiment and a plot from which the black crust has been removed for the seed-sowing experiment are shown in the foreground.
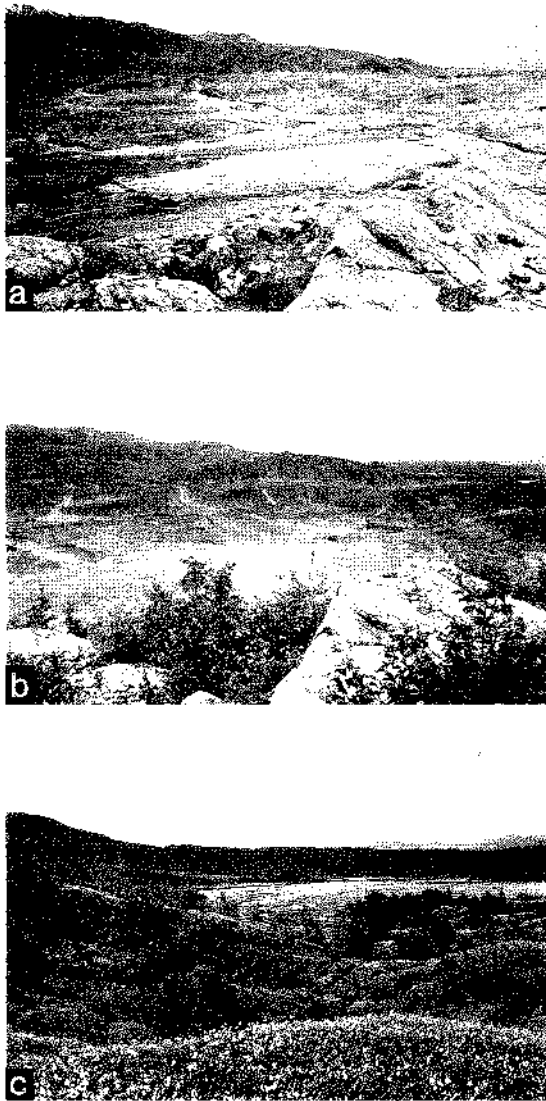
FIG. 3. *Dryas* stage (a) beneath the McBride Remnant in 1949 (center of photograph), (b) following deglaciation in 1967, and (c) at the beginning of the study in 1986. Photos from 1949 and 1967 courtesy of D. B. Lawrence.

Thus, our study areas were large areas of the major successional stages that had been previously studied to document successional change in the east arm of Glacier Bay.

METHODS

Experimental design

Within each of our four 2-km² study areas we chose 10 widely spaced sites that met the following criteria: dominance by the species of interest (pioneer, *Dryas*, alder, spruce), substrate of glacial till or outwash, <100 m elevation, moderate slope, presence of past succes-

sional research at a site, and infrequent use by park visitors. These sites encompassed natural variation in soil particle size and age within a successional stage. Because the glacier retreated linearly from the ocean to the upper bay, it was impossible to avoid pseudo-replication (Hurlbert 1984) in studying succession at Glacier Bay. Nonetheless, by selecting multiple sites within each stage we could compare variation in measured parameters within vs. between successional stages and thus minimize the sources of error associated with pseudoreplication. In all statistical analyses, we use the study site as our unit of replication. Our experimental design differs from that of most previous successional studies (but see Sondheim and Standish 1983, Messer 1988, Rydin and Borgegård 1991) in which a single site was chosen to represent each successional age.

Environment

At each site (*n* = 10 per successional stage) we collected a composite sample of the top 10 cm of mineral soil from several points. The soil was sieved (2 mm) and packed firmly into a soil tin of known volume to estimate bulk density of fine soil (g/cm³, dry mass) and soil moisture as mass loss, after oven drying at 65°C. This method of measuring bulk density permitted us to determine the relationship among soil parameters without the confounding influence of the large amount of rock and air spaces present in these soils. Soil pH was measured with a glass electrode on a saturated soil paste equilibrated with distilled water for 2 h. Particle size of air-dried soils was determined by the Bouyoucos hydrometer method, and organic content by mass loss on ignition at 400°C (Black 1965). Oven-dried samples were digested in selenous-sulfuric acid and analyzed colorimetrically for total N and P, using a Technicon autoanalyzer (Van Cleve et al. 1971).

To characterize nutrient pools at each stage, we collected a new set of samples by soil horizon and measured the amount of soil particles <2 mm per unit soil volume (which we term field bulk density) and its nutrient concentration at five sites per stage (the excavation method of Blake and Hartge 1986). After removing the organic horizon (a 2–5 mm algal crust in the pioneer stage, Fig. 2) from a 1 m² area, all mineral soil in the A + B horizons was sieved through a 10-mm mesh screen to remove large rocks and roots. The base of the B horizon was determined by color change from brown to a gray unmodified C horizon. The dimensions of the soil pit were carefully measured. In the laboratory, each sample (soil particles <10 mm) was weighed and thoroughly mixed, and a subsample was weighed, dried at 65°C, sieved through a 2-mm mesh screen, and reweighed to calculate the amount of soil particles <2 mm taken from the soil pit. This field bulk density is less than bulk density determined with soil tins because of the many rocks and air pockets in the glacial till. It is also less than the "bulk density
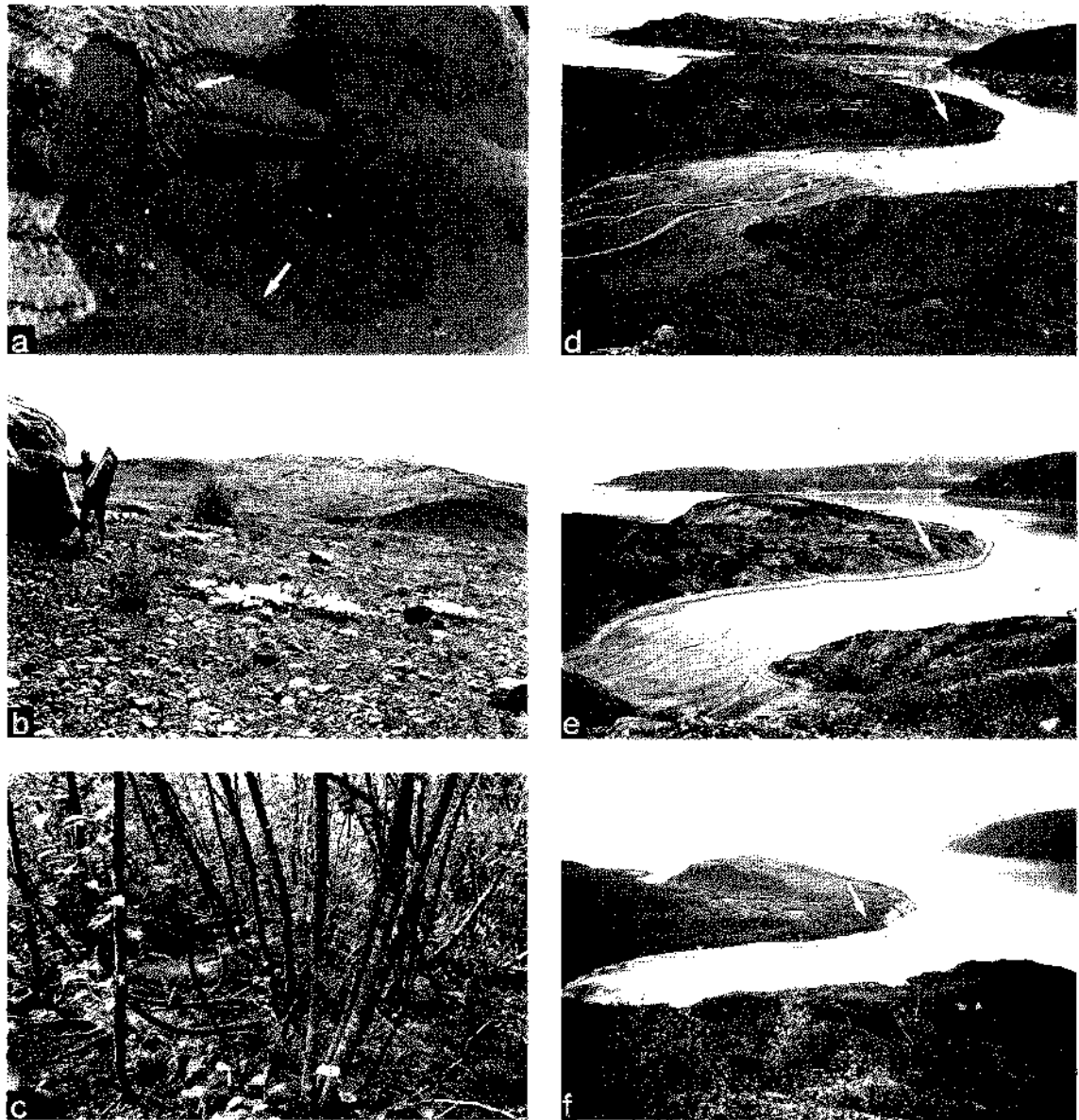
FIG. 4.   Alder stage (a) at the time of deglaciation in 1929 (arrows indicate the borders of the study area), (b) during transition from the pioneer to the *Dryas* stage in 1941, and (c) at the beginning of the study in 1986. View of the study area on the far (south) side of Nunatak cove in (d) 1949, (e) 1967, and (f) 1987. Arrows indicate the right-hand edge of the study area. Photo 4a courtesy of GBNPP; photos 4b, d, and e courtesy of D. B. Lawrence.

of fine earth" used by Crocker and Major (1955), Ugolini (1968), and Bormann and Sidle (1990), who subtracted out the volume of boulders in the till. Their bulk density is calculated on the volume of soil-plus-pore space (but not rocks) and is the standard method of calculating bulk density of forest soils; our field bulk density is based on the total excavated volume in our soil pits and is, therefore, more variable but more representative of the amount of soil and of nutrients present in the field. We estimated the volume of rocks plus macropores by comparing the field bulk density with the bulk density obtained by placing soil <2 mm in a

soil tin. A subsample of these soils was air-dried and analyzed for organic matter (mass loss on ignition), Olsen's extractable P, and total N (Black 1965). The remaining soil was saved for greenhouse pot tests. Pool size of nutrients was calculated as the product of field bulk density, soil depth, and nutrient concentration. Accumulation rate was calculated as the increase in pool size between successive stages divided by the difference in average age between stages.

In each stage we measured photosynthetically active radiation (400–700 nm) using a LI-COR quantum sensor on overcast days (typical weather) in mid-July 1988

FIG. 5. Spruce stage in 1988.

in the open and at 5-m intervals along 125-m transects through the understory (1.5 m height) of each stage.

Greenhouse pot tests

To ascertain successional changes in soil fertility and the identity of nutrients limiting to growth of spruce and alder in each stage, we collected soils from 5 sites/stage (see above, *Environment*) in July 1988 and shipped them immediately to Fairbanks, Alaska, where they were stored frozen for later greenhouse pot experiments. After determining the water content of each soil sample, we placed 1400 g dry-soil (<2 mm) equivalent into each of 4 pots/site in each of the following treatments: control, N, P, NP, and alder litter. Pots were given 5% Hoagland's solution, modified to exclude N and P (control and alder-litter treatments), exclude N (P treatment), exclude P (N treatment), or complete (NP treatment). N was provided as nitrate and ammonium, and KCl was added as necessary to maintain the same potassium content in all treatments (Van Cleve and Harrison 1985). Nutrient solutions were added every 2 wk at 25 mL/pot for 1 mo, 50 mL/pot for 2 mo, and 75 mL/pot (10% Hoagland's) for the final month to allow an increase in nutrient supply as seedling biomass and nutrient demand increased (Ingestad 1988). Any nutrient solution that leached through the pot was collected in a plastic saucer and added back to the pot when plants were next watered to maintain a closed nutrient cycle (Shaver and Melillo 1984). We used dilute nutrient solutions to maintain ecologically realistic concentrations of available nutrients. In the alder-litter treatment we mixed 7 g ground alder litter (3.44% N) into the top 3 cm of soil to double the amount of N estimated to be present in pioneer soil.

Half the pots in each treatment were seeded (12 viable seeds/pot) with alder and half with spruce seed collected in October 1988 in Gustavus, at the mouth of Glacier Bay. Pots were placed in a greenhouse in February 1989, with a 20:4 day : night photocycle and 20°:15°C day : night temperature regime, with light supplemented with mercury-vapor lamps. After seeding, pots were covered with plastic to minimize evaporation and watered daily. After 1 mo, percentage germination was determined, and pots were thinned to three spruce or two alder seedlings per pot. Pots were rearranged on the benches every 2 wk. After 4 mo growth, seedlings were harvested, washed free of soil, examined for presence of root nodules (alder only), separated into leaves, stems, and roots, oven-dried at 65°C, and weighed. The five sites per stage were used as our unit of replication, with two subsamples (pots) per treatment and site.

Life history traits

We collected seeds from at least 10 individuals of the dominant species from each successional stage (*Epilobium*, *Dryas*, alder, and spruce). From the bulked seed collection of each species we cleaned the seeds of any appendages and weighed five groups of 50 seeds/species.

We estimated age of first reproduction of alders by coring the base of the largest stem of shrubs that were currently producing cones but which had no old persistent cones ($n = 10$ individuals). For spruce, we could not tell whether a tree was producing cones for the first time. The ages given are ages of 20 of the smallest diameter reproductive trees cored in several successionally young stands and are probably an overestimate of age at first reproduction. To estimate the age at first reproduction of *Dryas*, we measured four radii on each of 15 marked clones in four successive years and developed an exponential regression model (diameter = $1.73e^{0.24\text{age}}$, $r^2 = 0.93$) of clone diameter against clone age, assuming that plant age was zero at zero size. Using this regression model, we estimated age at first reproduction from diameter of the smallest flowering individual we found. Our estimates seem reasonable in light of known surface ages. If growth of young *Dryas* seedlings is slower than that of larger clones, we may have underestimated age at first reproduction by 1–3 yr. Age at first reproduction of *Epilobium* is estimated from presence of flowering individuals on surfaces of known age.

Maximum longevity at Glacier Bay was estimated from maximum ages of surfaces where individuals were found (*Epilobium* and *Dryas*) or maximum ages of individuals cored at the base of the stem with an increment borer (alder and spruce). Because all these species are perennials, we assume they could grow older in the absence of competition. We may have underestimated the maximum age of alder, which continues to produce new stems after the initial stem dies. We may have overestimated the maximum age of *Epilobium* and *Dryas*, which may have established several years after the soil became ice free.

Maximum heights were recorded for individuals of each species growing in the field at Glacier Bay.

Seed arrival and germination

At each pioneer and *Dryas* site, we put out two 1.5-m² seed traps from September to May, 1987–1989. The seed traps were constructed from the shade cloth used in the transplant experiments described below. In each alder and spruce site we put out two plastic trays 0.134 m² in area from September to May, 1987–1989. Contents of each seed trap were collected, and a sample of 50 seeds (or as many as were present, if <50) was counted and set aside to determine percentage germination at 20°C. The litter contained in the seed traps was air-dried, and all seeds of spruce and alder were separated from litter and counted to estimate total seed rain for each seed trap. Litter from each trap was separated into wood + cones and leaf litter and weighed to document litterfall. In the alder site leaf litter was analyzed for N and P to document annual aboveground nutrient input.

Cones of alder and spruce were collected in Gustavus in October 1987. Cones were air-dried, and seeds removed, cleaned, and stored frozen. Samples of seeds were germinated at room temperature or stratified on moist filter paper at 5°C for 1 mo, then germinated at room temperature to determine percentage seed viability. Cold stratification improved germination only for spruce. After determining average seed mass on five groups of 50 seeds, samples of 320 germinable alder seeds were kept frozen, and 500 germinable spruce seeds were cold stratified (5°C) on moist filter paper in petri dishes for 1 mo. At each site we established two 0.25-m² plots, one on undisturbed substrate, and one from which the overlying organic horizon was removed. Within each plot six subplots were established in late May/early June of 1988: two were seeded with spruce, two with alder, and two unseeded controls. Plots were revisited after 2, 4, 6, and 14 wk in 1988 and in late May and early August in 1989, at which times we counted the number of spruce and alder seedlings in each subplot. Data were pooled for the two subplots per species, site, and treatment, and the number of seedlings in control subplots was subtracted from the number of seedlings in the seeded subplots. Maximum seedling number was used as a measure of field germination (Walker et al. 1986), and the number of seedlings surviving to the end of the 2-yr study (as a percentage of maximum seedling number) was used as a measure of survivorship. In August 1989, we harvested six 1-yr and six 2-yr seedlings per species, site, and treatment (or as many as were present, if survivorship was low), washed all soil from the roots, measured total length of root and shoot, oven-dried, and weighed them. All remaining seedlings were destroyed, so as not to alter natural patterns of seedling establishment and succession at these sites.

To control for site variation in climate and seed predation, we collected mineral soil from five sites per stage and measured percentage germination of 12 viable alder or spruce seeds sown on these soils in a greenhouse (see *Greenhouse pot tests,* above). Two pots per site had pure mineral soil, and two pots per site had ground alder litter added to test for allelopathic effects. Percentage germination was measured after 1 mo.

Natural seedlings

In August 1988 we harvested ≈10 naturally occurring spruce seedlings from each stage. In the pioneer stage we sampled spruce seedlings from the south side of Muir Inlet (across the inlet from our pioneer site: site P in Fig. 1) where spruce seedlings were more abundant but plant cover was still low (<5%). Care was taken to collect as much of the root system of each seedling as possible. After harvest, seedling age was determined by counting annual rings at the base of the shoot. These ring counts were always greater than the number of detectable branch whorls. Shoots of each year class were separated, and mass of wood and needles determined. Ln(mass per unit length) of all stem segments (excluding the main stem below the lowest whorl of branches) was regressed against age of stem segment to estimate secondary wood production (Shaver 1986). This was added to the mass of current-year's stems and needles to estimate aboveground production. Approximately 500 stem segments were measured on seedlings from each successional stage, and mean values for each stem age class were used in the regression analysis. Needles and stems from each seedling were separately ground in a Wiley mill (850 μm mesh screen), digested in sulfuric acid and hydrogen peroxide with a $CuSO_4$ catalyst, and analyzed colorimetrically for N and P with a Lachat Ion Flow Analyzer (Pugnaire and Chapin 1993).

Seedling transplants

Spruce seeds were collected at Gustavus in September 1983, cleaned, and stored frozen. (There were too few alder seeds to collect in 1983.) In April 1984 spruce seeds were sown in 440-cm³ "conetainers" in a 1:1 medium of *Sphagnum* peat moss and coarse vermiculite and grown in a greenhouse at the U.S. Forest Service nursery at Petersburg, Alaska, 250 km south of Glacier Bay. Alder seeds were collected at Gustavus in October 1984 and sown at Petersburg in March 1985. Plants were watered with a dilute Hoagland's solution except in the final year, when seedlings overwintered under snow and grew the subsequent year outside with no additional nutrient input.

In August 1986, seedlings were shipped to Glacier Bay and transplanted into our 10 study sites in each successional stage (pioneer, *Dryas,* alder, and spruce). In each site six 1.5 × 1.5 m plots were selected that contained no trees or erect shrubs. The six plots were randomly assigned to one control and two treatment plots for both spruce and alder. In each treatment plot we planted six alder or six spruce seedlings, and in each

control plot we planted eight alder or spruce seedlings in a grid with 50-cm spacing. Each seedling was individually identified so that we could follow its growth in subsequent years.

For both alder and spruce seedlings, there were control and alder-litter plots in each of the four stages, shaded plots (to simulate shading by alder) in the pioneer and *Dryas* stages, and trenched plots (to remove root competition by woody species) in the alder and spruce stages. Plots in the *Dryas* stage were located at least 10 m from any of the scattered alders present at these sites. In addition, eight spruce seedlings were planted near (within 1 m of the root crown) isolated naturally occurring alders in the *Dryas* stage. Across Muir Inlet from our pioneer site was an area where scattered alders had invaded (see *Natural seedlings*, above). Here we planted 40 spruce seedlings near (within 1 m) alders and another 40 spruce seedlings far (at least 10 m) from alders. Twenty seedlings of each species were harvested at the time of transplanting, separated into leaves, stem, and roots, oven-dried, and analyzed for N and P. At the time of transplant, spruce seedlings had abundant ectomycorrhizal mantles, and alders were nodulated.

In the alder-litter plots, we annually applied 145 g/m^2 of ground alder litter (3.44% N, giving an annual N addition of 5.3 g/m^2, the average annual N input during the alder stage of succession estimated by Crocker and Major [1955]). Alder litter was added to plots in May 1987, 1988, and 1989 over an area that extended 0.25 m beyond the seedling transplants in all directions. This alder litter was collected at Gustavus in September 1986 and 1988, air-dried, ground in a Wiley mill, and a subsample analyzed for N and P. Shaded plots were covered by optically neutral greenhouse shade cloth that removed 66% of photosynthetically active radiation (400–700 nm), confirmed with a LI-COR quantum sensor placed beneath these shade frames. Each shade frame was designed with an overlapping roof and a wall, the lower edge of which was ≈10 cm above the soil surface, to provide maximum air circulation without direct radiation (Fig. 2). For 3 yr, beginning in 1987, shade cloths were set up in May and removed in September. In May 1987, ditches were dug around each trenched plot to a depth of 50 cm (below 99% of the roots of alder or spruce), lined with two layers of 0.15 mm thick plastic, and refilled with soil. On two sides of each trenched plot we counted the number of coarse roots (> 1 mm diameter) cut by the trench in 15 × 50 cm vertical transects to determine the vertical distribution of roots. We also measured the thickness of the litter and organic horizon in each of 10 sites in the alder and spruce stages.

Each September we recorded number of surviving seedlings and total height and height increment (length of current growth) of the leader (the tallest shoot) of each seedling transplant in each plot. Data presented are annual height increment and total change in height during the 3-yr growth period. Total height growth during the experiment can be less than the sum of annual height increments when summer growth increment is balanced by overwinter death of the leader.

After 3 yr of growth in the treatments (August 1989) we harvested all surviving seedlings (except 3–4 control spruce seedlings per site, which were left for future study). Although care was taken to collect all major roots and as much fine root material as possible, some fine roots were inevitably lost. Roots were washed and dead stems discarded before dividing each seedling into current-year's leaves, current-year's stems, old leaves (spruce only), old stems, and roots. Samples were weighed after oven drying to constant mass at 65°C. In addition to the mass of each plant part, we calculated the following parameters for each seedling: root : shoot ratio, current growth (current leaves + current stem), and aboveground relative growth rate {[ln(aboveground biomass) − ln(aboveground biomass − current growth)]/1 yr}. Aboveground current growth and relative growth rates do not include secondary stem growth.

After weighing, we systematically selected two or more seedlings from each plot in alternate sites (i.e., five sites per stage) and analyzed each plant part for nutrients (see *Natural seedlings*, above). These tissue nutrient data were multiplied by corresponding site means of tissue biomass to calculate tissue nutrient pool in each plant part and total nutrient pool per plant for each site. These nutrient pools were compared with those of seedlings harvested at the time of transplant. Relative accumulation rate was calculated from nutrient pools in new growth and total aboveground biomass, in a fashion analogous to relative growth rate.

Alder effect on Dryas

To determine why *Dryas* disappears after invasion by alder, we established in May 1987 four treatments in alder-free areas within each *Dryas* site: control, shade (66% light reduction), ground alder litter (chemical effect of litter), and unground alder litter (chemical plus physical effect of litter). Air-dried alder litter, either unground or ground in a Wiley mill, was applied at a rate of 145 g/m^2 in 0.5 m^2 plots. All plots were covered by bridal veil (4-mm mesh) to hold litter in place without altering light regime. Shoots grew above the added litter each year, so additional litter was applied at the same rate each May, 1987–1989. In August 1989 we harvested aboveground biomass of *Dryas* from 0.125-m^2 plots in each treatment, separated it into leaves, stems, and inflorescences, dried it at 65°C, and weighed it.

Statistical analyses

For those parameters where multiple samples were measured at each of 10 replicate sites per successional stage (seed rain, litterfall, seed germination and growth, seedling transplant data), the within-site data were

TABLE 1. Site age and environmental characteristics in the four major successional stages in Glacier Bay. Except for soil texture (measured in upper 10 cm of mineral soil), parameters were measured in the A + B horizons. Data are means ± 1 SE, n = 10 sites/stage. ND indicates no data collected. Within rows, values followed by the same letter are not significantly different (P > .05).

	Successional stage			
Parameter	Pioneer	Dryas	Alder	Spruce
Site age (yr)*	5–10	35–45	60–70	200–225
Soil texture (% of total)†				
Sand	74.6 ± 4.3[a]	90.6 ± 2.6[b]	64.8 ± 1.9[a]	69.4 ± 2.1[a]
Silt	15.8 ± 2.8[b]	7.2 ± 1.7[a]	24.7 ± 1.5[c]	22.5 ± 1.6[bc]
Clay	9.6 ± 1.8[b]	2.3 ± 0.9[a]	10.5 ± 0.7[b]	8.1 ± 0.7[b]
Soil depth (cm/horizon)				
Litter	0[a]	ND	1.7 ± 0.2[b]	3.2 ± 0.2‡[c]
Organic horizon	0[a]	ND	2.8 ± 0.8[b]	8.0 ± 1.9[c]
A + B horizons§	5.2 ± 0.5[a]	7.0 ± 0.7[a]	8.8 ± 0.2[a]	15.1 ± 2.5[b]
Field bulk density (g/cm³)§	0.48 ± 0.10[a]	0.35 ± 0.06[a]	0.44 ± 0.03[a]	0.70 ± 0.22[a]
Soil (% of volume)	28	22	26	62
Soil pools§				
Soil (kg/m²)	24.7 ± 6.5[a]	24.5 ± 5.5[a]	37.6 ± 2.6[a]	97.0 ± 35.1[a]
Carbon (kg/m²)	1.3 ± 0.4[a]	1.3 ± 0.3[a]	2.9 ± 0.2[a]	9.7 ± 2.6[b]
Nitrogen (g/m²)	3.8 ± 0.8[a]	5.3 ± 1.1[a]	21.8 ± 3.4[a]	53.3 ± 14.0[b]
Accumulation rate (g·m⁻²·yr⁻¹)				
Carbon	ND	0	80	41
Nitrogen	ND	0.07	0.83	0.18
Root density (no./dm³)§				
0–10 cm	0[a]	ND	9.6 ± 1.0[b]	11.5 ± 0.8[b]
10–20 cm	0[a]	ND	5.1 ± 0.7[b]	9.9 ± 0.8[c]
20–30 cm	0[a]	ND	2.9 ± 0.6[b]	2.9 ± 0.5[b]
30–40 cm	0[a]	ND	1.7 ± 0.5[b]	0.8 ± 0.2[b]
40–50 cm	0[a]	ND	0.1 ± 0.1[a]	0.1 ± 0.1[a]
Irradiance at noon (photon flux, µmol·m⁻²·s⁻¹)	510 ± 17[a]	ND	34 ± 2[b]	40 ± 7[b]

* Time since deglaciation.
† Upper 10 cm of mineral soil.
‡ Moss.
§ A + B horizons combined.

nested as subsamples within the site, so that the site is the unit of replication in all statistical tests (n = 10 sites per successional stage unless otherwise noted). The significance level in all tests was P ≤ .05, and means are presented ±1 SE.

To determine whether environmental factors and plant responses differed among our four successional stages, we used nested two-way analyses of variance (ANOVA) with 10 study sites (random effect) nested within successional stage (fixed effect). If a stage effect was significant, stages were compared with Ryan's Q test, which controlled the experimentwise error rate at P ≤ .05 (Day and Quinn 1989). The effect of experimental treatments (shade, alder-litter addition, root trenching, proximity to alder shrubs) on plant response within each successional stage was determined with stage-specific two-way ANOVAs with site (random block effect) and treatment (fixed effect) crossed. If a treatment effect was significant, each treatment was compared to a control using a two-tailed Dunnett's test, which controlled the experimentwise error rate at P ≤ .05. The effects of two seedbed types in field and greenhouse seed-sowing trials were compared with t tests.

The greenhouse experiment, soil nutrient pools, and the nutrient pools in seedling transplants had the same basic design and were analyzed statistically as described above with a sample size of five. Linear regression of annual height increment of seedling transplant against measurement year were used to detect significant year-to-year growth trends.

Prior to analysis, measured values were transformed to minimize heteroscedasticity if their means per study site within a successional stage were significantly (P ≤ .05) correlated with their variances.

RESULTS

Environment

Mineral soils from the pioneer, alder, and spruce stages were silty loams of similar texture (Table 1), although the pioneer soils had slightly less silt than soils from the two oldest stages. By contrast, soils from the Dryas stages had more sand and correspondingly less clay and silt than soils from other stages.

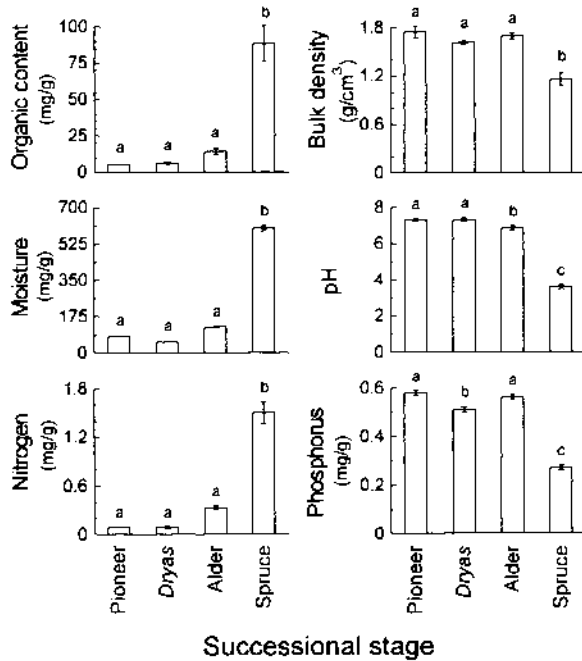The pioneer and Dryas stages were similar to one another in organic content, soil bulk density, soil

FIG. 6. Soil properties of the upper 10 cm of mineral soil at four successional stages. Data are means ± 1 SE, $n = 10$ sites per stage. For each parameter, means with the same letter are not significantly ($P > .05$) different.

moisture, pH, and total N (Fig. 6). Compared to these early-successional soils, spruce soils had higher organic content associated with decreased soil bulk density, increased soil moisture, lower pH, and higher total N. The alder soils tended to be intermediate between the early successional and spruce soils. Total soil P was highest in the pioneer and alder soils and declined by 50% in the late-successional spruce soils. Available P was <1 mg/kg in all sites (data not shown).

When total soil pools were examined over the complete A + B horizons, results were highly variable due to spatial heterogeneity in amount of rocks in the glacial till and depth of profile development. However, the following patterns emerged (Table 1): less than a third of the soil volume was occupied by soil <2 mm in all except the spruce stage. The rest of the volume was occupied by rocks, roots, and large air pockets beneath rocks. The pioneer and Dryas stages were sim-

ilar to one another in soil pools of C and N, but these pools increased in size with progression to the alder (strong nonsignificant trend) and spruce stages. Both C and N accumulated most rapidly from the Dryas to the alder stage and continued to accumulate in the spruce stage.

Annual litterfall from trees and erect shrubs was <4 g/m² in the pioneer and Dryas sites and ≈250–300 g/m² in the alder and spruce stages (Table 2). In the alder stage, the annual nutrient throughput as fine litter was 9.7 ± 0.4 g·m⁻²·yr⁻¹ for N and 0.52 ± 0.02 g·m⁻²·yr⁻¹ for P.

Irradiance at seedling height was reduced >10-fold by the alder and spruce canopies (Table 1).

Greenhouse seedling growth

When spruce seedlings were grown in the greenhouse on mineral soils from each successional stage, pioneer soils tended to support least growth, Dryas and alder soils intermediate growth, and spruce soils the most growth (Table 3), indicating that unfavorable soil conditions contribute to slow plant growth in early succession. Root : shoot ratio was highest in the Dryas soils and showed no clear correlation with seedling growth.

Nutrient addition had no significant effect on spruce growth in soil from the pioneer stage, although N and P together tended to stimulate growth. Phosphorus stimulated growth in the alder and spruce soils, suggesting P limitation in soils that were presently or previously occupied by N-fixing alder. Pioneer soils also showed least seedling growth response to nutrient addition, suggesting that some soil factor in addition to N and P limited growth of spruce seedlings in early successional soils. Addition of alder litter tended to inhibit spruce growth in the pioneer soils and had no significant effect on spruce growth in other soils, indicating that over the 4-mo time frame of our experiment alder litter did not facilitate growth of spruce seedlings.

Alder seedlings were more sensitive to differences in soils than were spruce seedlings. Alder biomass increased from pioneer and alder to Dryas to spruce soils, showing a 250-fold range in biomass across these soil types (Table 3). Root : shoot ratio declined, as biomass increased across these soils. Nodulation was greatest in those soils that supported greatest growth and was

TABLE 2. Litterfall of trees and shrubs of the four major successional stages at Glacier Bay. Data are means ± 1 SE, $n = 10$ sites/stage, 2 litter traps/stage. ND indicates no data collected. Statistics as in Table 1.

Year	Litter type	Litterfall (g·m⁻²·yr⁻¹)			
		Pioneer stage	Dryas stage	Alder stage	Spruce stage
1987	Fine litter	1.3 ± 0.4ᵃ	2.5 ± 0.6ᵃ	203 ± 8ᶜ	98 ± 8ᵇ
	Wood	0ᵃ	0ᵃ	45 ± 9ᵇ	152 ± 64ᶜ
	Total litter	1.3 ± 0.4ᵃ	2.5 ± 0.6ᵃ	248 ± 12ᵇ	250 ± 69ᵇ
1988	Fine litter	1.8 ± 0.4ᵃ	3.0 ± 2.2ᵃ	260 ± 11ᵇ	ND
	Wood	0ᵃ	0ᵃ	47 ± 6ᵇ	ND
	Total litter	1.8 ± 0.4ᵃ	3.0 ± 2.2ᵃ	307 ± 13ᵇ	272 ± 34ᵇ

TABLE 3. Biomass, root:shoot ratio, and percentage nodulation of spruce and alder seedlings grown in the greenhouse on soils from each successional stage amended with nitrogen and/or phosphorus. Another treatment had alder litter mixed with the soil. Data are means ± 1 SE, $n = 5$ sites/stage, 2 pots/site. In the control treatment, values with the same letter are not significantly different ($P > .05$). Significant treatment effects ($P < .05$) within a stage are also indicated (*).

Species Parameter Treatment	Successional stage			
	Pioneer	*Dryas*	Alder	Spruce
Spruce				
Biomass (mg/plant)				
Control	27 ± 2[a]	41 ± 3[a]	43 ± 5[a]	147 ± 29[b]
N	29 ± 2	45 ± 6	43 ± 5	154 ± 22
P	26 ± 3	55 ± 6	69 ± 15*	258 ± 53*
NP	36 ± 8	64 ± 6	67 ± 7*	276 ± 61*
Litter	22 ± 1	45 ± 11	50 ± 5	159 ± 50
Root:shoot ratio				
Control	0.66 ± 0.06[a]	0.93 ± 0.07[b]	0.75 ± 0.06[ab]	0.74 ± 0.09[a]
N	0.62 ± 0.05	0.73 ± 0.03	0.63 ± 0.05*	0.56 ± 0.06
P	0.65 ± 0.05	0.85 ± 0.04	0.65 ± 0.05	0.64 ± 0.07
NP	0.50 ± 0.03	0.70 ± 0.05*	0.58 ± 0.04*	0.57 ± 0.04
Litter	0.64 ± 0.06	0.70 ± 0.05*	0.60 ± 0.05*	0.55 ± 0.03
Alder				
Biomass (mg/plant)				
Control	13 ± 2[a]	1567 ± 317[b]	298 ± 181[a]	3225 ± 583[c]
N	41 ± 24	2009 ± 351	823 ± 424	3258 ± 342
P	22 ± 6	920 ± 254	1110 ± 419	3499 ± 322
NP	21 ± 7	1924 ± 204	955 ± 425	3146 ± 377
Litter	16 ± 3	1262 ± 256	647 ± 326	2852 ± 336
Root:shoot ratio				
Control	0.97 ± 0.10[a]	0.55 ± 0.07[bc]	0.71 ± 0.13[b]	0.42 ± 0.05[c]
N	1.36 ± 0.22	0.55 ± 0.06	0.62 ± 0.10	0.42 ± 0.03
P	0.87 ± 0.11	0.61 ± 0.09	0.44 ± 0.03	0.39 ± 0.06
NP	1.16 ± 0.34	0.45 ± 0.03	0.52 ± 0.06	0.44 ± 0.07
Litter	0.90 ± 0.09	0.63 ± 0.05	0.54 ± 0.08	0.39 ± 0.03
Nodulation (% of pots)				
Control	0	100	44	100
N	0	100	67	100
P	25	100	78	100
NP	10	100	50	100
Litter	43	90	80	100

absent in the pioneer soils unless supplemented with alder litter or P. Thus, the rapid growth of alder shrubs that colonize the pioneer stage in the field depended on nodulation conditions that were not met in our greenhouse experiment. Due to high variability among replicate pots, there was no effect of added nutrients or alder litter on alder growth or allocation in any soil type.

Life history traits

The seeds of early-successional species (*Epilobium, Dryas*) were lighter than those of mid-successional species (*Alnus*), while the late-successional spruce had the heaviest seeds (Table 4), suggesting that ease of dispersal contributes to the successional pattern at Glacier Bay. Moreover, seeds of many early- and mid-successional species (e.g., *Epilobium, Dryas, Salix, Populus*) have hairy appendages that aid dispersal. Early-successional colonists (e.g., *Dryas, Epilobium*) differed from mid- and late-successional species in having a younger age at first reproduction, shorter life-span, and shorter maximum height (Table 4).

Seed rain and initial establishment

In our 2 yr of measurement, we found no spruce seeds and negligible alder seeds in the pioneer stage

TABLE 4. Life history traits of plants that dominate different successional stages. Data are means ± SE, sample size in parentheses. Values of seed mass with the same letter are not significantly different ($P > .05$).

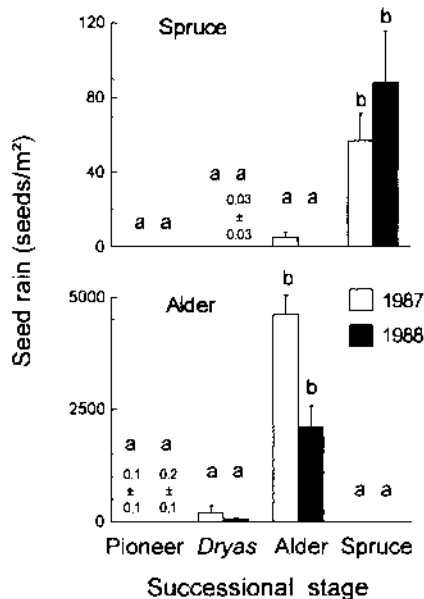| Species	Successional stage	Seed mass (μg/seed)	Maximum height (m)	Age at first reproduction (yr)	Maximum longevity (yr)
Epilobium latifolium	Pioneer	72 ± 5 (5)[a]	0.3	1–2	20
Dryas drummondii	Dryas	97 ± 18 (5)[a]	0.1	6–8 (15)	50
Alnus sinuata	Alder	494 ± 23 (5)[b]	4	8.1 ± 0.6 (10)	100
Picea sitchensis	Spruce	2694 ± 26 (5)[c]	40	30–50 (20)	700

FIG. 7. Seed rain of spruce and alder in four successional stages in 1987 and 1988. Data are means and 1 SE, $n = 10$ sites per stage. Within years, means with the same letter do not differ significantly ($P > .05$).

(Fig. 7). This area was ≈ 10 km from the nearest cone-bearing spruce and 3 km (across Muir Inlet) from the nearest stand of reproductive alders, although widely scattered cone-bearing alders grew within 1 km of the study area. As expected, spruce seed rain was most abundant in the spruce stage, and alder seed rain was most abundant in the alder stage. Both species also had low (spruce) to moderate (alder) seed rain in the stage that preceded the stage in which they dominated, pre-sumably coming from the scattered reproductive alders in the *Dryas* stage and the scattered reproductive spruce in the alder stage. This suggests that nucleation (initial establishment of a few outlier individuals that provide local seed rain) is an important source of seeds for successional change (Cooper 1923b, 1931, Yarranton and Morrison 1974). Germination of alder seeds (32 ± 3% in 1988 and 21 ± 4% in 1989) did not differ between seeds collected from seed traps in the *Dryas* and alder stages, but none of the alder seeds from the pioneer stage germinated, suggesting that seeds trans-ported long distances from the parent plant are less likely to be viable.

On undisturbed seedbeds, sown spruce seeds had highest germination in the pioneer and spruce stages, and alder produced significant numbers of germinants only in the pioneer stage (Fig. 8). Only in the pioneer stage was there significant survivorship of germinants of either species in undisturbed seedbeds. Removal of surface litter and organic layers had no significant effect on spruce germination in any stage (except a small stimulation in the alder stage). However, litter removal enhanced (or tended to enhance) survivorship in all

except the pioneer stage, where removal of the black crust reduced survivorship by 41%. Removal of the surface organic mat increased number of alder ger-minants in the *Dryas* and spruce stages. As with spruce, organic-mat removal increased survivorship of alder in the spruce stage but tended to reduce survivorship in the pioneer stage. These results indicate that all later stages inhibited initial seedling establishment of spruce and alder relative to the pioneer stage, in part due to the presence of overlying litter and organic horizons. By contrast, the thin algal crust of the pioneer stage tended to inhibit germination but facilitate survivor-ship. Maximum spruce germination occurred late the 1st yr of sowing, whereas alder continued to germinate in the 2nd yr (data not shown).

Those germinants of spruce and alder that survived achieved greater mass in the pioneer or *Dryas* stages than in stages with a closed canopy (Fig. 8). The fact
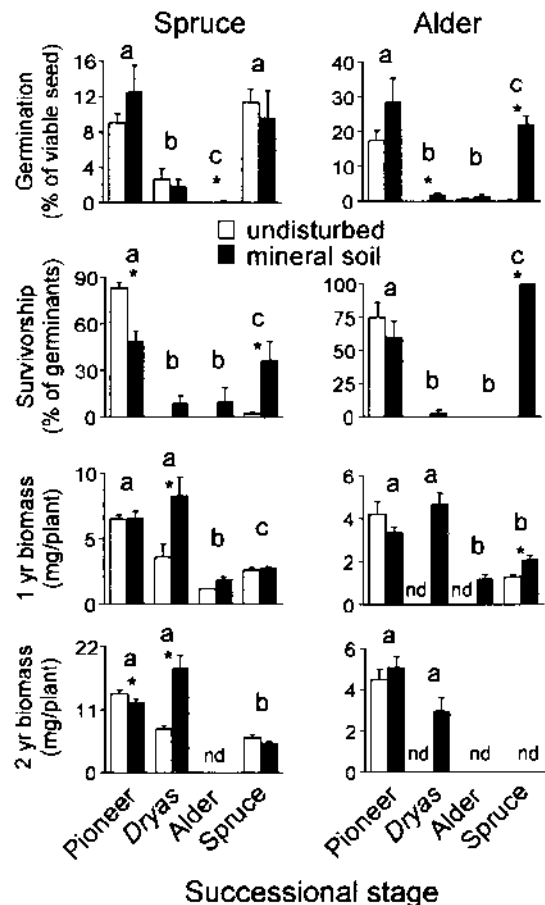
FIG. 8. Germination, survivorship, and biomass of 1-yr-and 2-yr-old seedlings of spruce and alder sown on undis-turbed (open bars) and mineral (solid bars) soil surfaces in four successional stages. Data are means and 1 SE, $n = 10$ sites per stage. Means (both treatments combined) at each stage with the same letter are not significantly different ($P > .05$). Significant treatment differences are also indicated (*). In some stages no seedlings survived or none were harvested (ND).

TABLE 5. Ratio of root length to shoot length of spruce and alder seedlings growing from sown seed in the four major successional stages at Glacier Bay. Seedlings were collected 1 and 2 yr after germination on undisturbed or mineral-soil seedbed. Data are means ± 1 SE; sample size (number of sites; shown in parentheses) varied because all seedlings died in many sites. Root:shoot ratios for both treatments combined differ among stages labeled with different letters ($P < .05$). Significant effects of seedbed are also shown (*).

Species	Seedling age	Seedbed type	Root:shoot length ratio			
			Pioneer stage	Dryas stage	Alder stage	Spruce stage
			a	ab	b	c
Spruce	1 yr	Undisturbed	1.9 ± 0.2 (9)	1.1 ± 0.2 (4)	1.1 (1)	0.9 ± 0.1 (9)
		Mineral	2.8 ± 0.3 (7)*	3.7 ± 0.7 (4)*	1.4 ± 0.2 (6)	0.7 ± 0.1 (10)
			a	a		b
	2 yr	Undisturbed	2.5 ± 0.2 (10)	1.6 ± 0.4 (2)	(0)	0.9 ± 0.1 (6)
		Mineral	2.8 ± 0.2 (10)	2.5 ± 0.5 (4)	(0)	0.5 ± 0.1 (7)*
			a	a	b	c
Alder	1 yr	Undisturbed	6.4 ± 1.1 (4)	(0)	(0)	1.3 ± 0.2 (9)
		Mineral	6.2 ± 1.2 (4)	8.2 ± 1.4 (3)	1.1 ± 0.3 (6)	1.6 ± 0.1 (10)
			a	b		
	2 yr	Undisturbed	6.2 ± 0.8 (9)	(0)	(0)	(0)
		Mineral	5.4 ± 0.7 (8)	3.0 ± 0.2 (2)	(0)	(0)

that seedlings allocated a greater proportion of their length above ground in the later stages (i.e., lower root:shoot length ratio; Table 5) suggests that the decline in germinant growth in late succession was due more to shading than to a decline in belowground resources. These results indicate an inhibitory effect of alder and spruce stages on initial germinant growth of both spruce and alder.

The seed-sowing experiments were repeated in the greenhouse to control for stage differences in seed/seedling predation and microclimate. When seeds were sown on mineral soils in the greenhouse, germination rates were consistently higher in the greenhouse (Table 6) than on mineral soils in the field (Fig. 8) for both species in each stage. In the greenhouse, fewer spruce germinated on soil from the spruce stage, and fewer alder germinated on soil from the alder stage (Table 6). Otherwise successional stage had no significant effect on germination. This indicates that (1) germination of both spruce and alder was inhibited by soils from the stage in which each dominated, and (2) the low field germination on mineral soil was due, in part, to factors other than simple physical or chemical effects of the soils on germination. When alder litter was added to soils in the greenhouse, there was a strong inhibitory

effect on spruce germination, particularly in the pioneer and Dryas soils. Alder germination was inhibited by addition of alder litter only in pioneer soils. These results suggest an allelopathic effect of alder litter on germination. However, this effect may not be long lived, because unmodified soil from the alder site supported high germination of spruce (although not of alder).

Natural seedlings

Naturally occurring spruce seedlings were largest in the Dryas and alder stages and smallest in the spruce stage (Fig. 9), indicating that, for those seedlings that successfully establish, Dryas and alder stages tended to facilitate spruce biomass relative to the pioneer stage, and that the spruce stage inhibited biomass accumulation of spruce seedlings relative to earlier successional stages. Although harvested spruce seedlings in the Dryas and spruce stages were ≈4 yr younger than those in the pioneer and alder stages (Table 7), these age differences could not alone account for the differences among stages in seedling mass. Root:shoot ratio tended to be lowest in the alder stage and highest in the pioneer stage (Table 7), as expected from presumed stage differences in nutrient and light availability. As with biomass, apical and secondary stem growth and

TABLE 6. Germination of spruce and alder seeds in a greenhouse on mineral soil (control) or mineral soil amended with alder litter. Soils were collected from the A + B horizons in the four major successional stages at Glacier Bay. Data are means ± 1 SE, $n = 5$ sites/stage, 2 pots/site. Statistics as in Table 5.

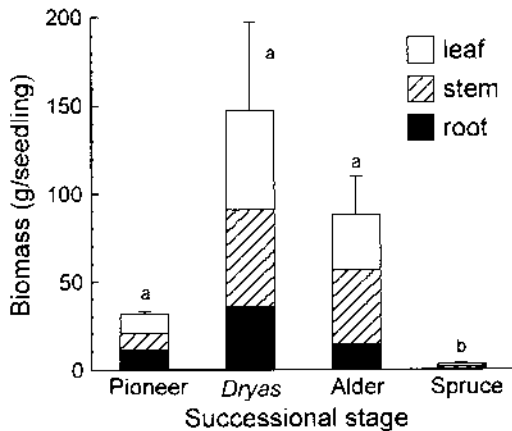| Species	Treatment	Germination (% of viable seeds)			
		Pioneer stage	Dryas stage	Alder stage	Spruce stage
		a	a	a	b
Spruce	Control	65 ± 5	60 ± 5	70 ± 5	34 ± 3
	+ alder litter	21 ± 3*	20 ± 3*	42 ± 6*	25 ± 5
		a	b	c	ab
Alder	Control	49 ± 5	35 ± 4	24 ± 3	44 ± 4
	+ alder litter	24 ± 4*	23 ± 8	30 ± 6	36 ± 7

FIG. 9. Biomass of roots, stems, and leaves of naturally occurring spruce seedlings in four successional stages. Data are means and 1 SE of total biomass. Sample sizes are given in Table 7. Means of total seedling biomass with the same letter are not significantly different ($P > .05$).

aboveground relative growth rate (RGR) were most rapid in the *Dryas* and alder stages, and tissue concentrations, pool sizes, and relative accumulation rates (RAR) of N and P tended to increase from the pioneer to the *Dryas* and alder stages (Table 7), indicating facilitation of nutrient uptake and growth of natural spruce seedlings in the *Dryas* stage.

Seedling transplants

Spruce. —Spruce seedlings transplanted into each successional stage for 3 yr were facilitated by the *Dryas* and alder stages and inhibited by the spruce stage relative to seedlings growing in the preceding stage. This pattern was generally shown for total seedling mass, aboveground production, RGR, and total height growth (Fig. 10, Tables 8 and 9) and is similar to the pattern observed with naturally occurring seedlings (Fig. 9, Table 7). Seedlings grew most rapidly and achieved largest biomass in the alder stage. The large height increment in the alder stage (Table 9) reflects rapid growth, but the substantial height increment in the spruce stage may be an etiolation response because biomass, growth rate, and aboveground production of spruce seedlings in the spruce stage were considerably less than in the preceding (alder) stage. Seedling biomass in the spruce stage did not increase significantly over the 3-yr period following transplanting. In the pioneer and *Dryas* stages, height growth of spruce declined in each successive year (Table 9), suggesting that much of the initial (and total) height growth was supported from reserves acquired before transplanting. By contrast, in the alder stage height growth of spruce increased in each successive year, indicating a strong facilitative effect, associated with the exponential growth of seedlings commonly found under favorable conditions. There was negligible mortality of spruce seedlings over the 3-yr

study in any successional stage. As with the trend in germinants and naturally occurring seedlings, root: shoot ratio was higher in the pioneer and *Dryas* stages than in the alder and spruce stages, reflecting low availability of soil resources and high availability of light in the early stages.

Concentration of N in current-year's needles increased substantially from the pioneer to the *Dryas* to the alder stage but declined in the spruce stage (Table 10), in parallel with the patterns described above for growth. Needle P concentration was higher in the alder and spruce stages than in the pioneer and *Dryas* stages. The low N:P ratio in the pioneer stage (3.4) suggested that N was more deficient (or P less deficient) in early succession. Spruce seedlings in the alder stage more than doubled their total N pool during the 3-yr experiment, whereas seedlings in the pioneer and spruce stages lost N, due to some combination of leaching, tissue turnover, and our incomplete recovery of fine roots (Fig. 11, Table 11). Changes in seedling P pool during the experiment were less pronounced than those of N, but generally followed a similar pattern among stages.

Our manipulations provided insight into the causes of changes in growth of spruce seedlings through succession. Addition of alder litter at half the rate observed in the alder stage caused an increase in total biomass, aboveground production, RGR, and height growth (nonsignificant trend) of spruce seedlings in the pioneer and *Dryas* stages but had no effect on these parameters in the alder and spruce stages (Table 8). Seedling nu-
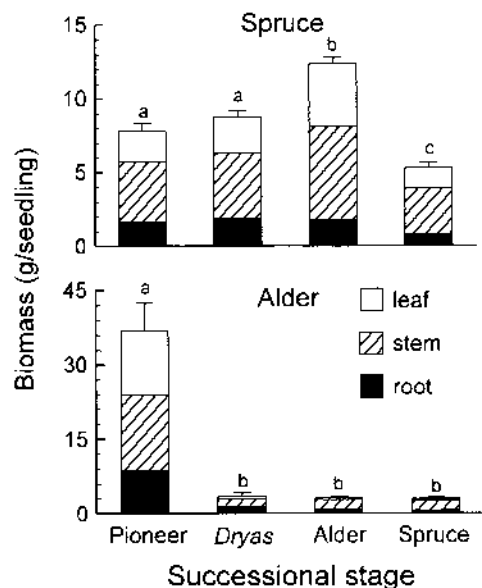

FIG. 10. Biomass of roots, stems, and leaves of control spruce and alder seedlings transplanted into four successional stages. Data are means (and 1 SE of total seedling biomass), $n = 10$ sites per stage. Means of total seedling biomass with the same letter are not significantly different ($P > .05$).

TABLE 7. Growth and nutritional characteristics of naturally occurring seedlings in the four major successional stages at Glacier Bay. Data are means $\pm$ 1 SE. Values for a measure with the same letter are not significantly different ($P > .05$).

Parameter	Successional stage			
	Pioneer	*Dryas*	Alder	Spruce
Seedling age (yr)	13.3 ± 0.9^a	9.5 ± 0.8^b	12.7 ± 1.1^{ab}	8.9 ± 0.7^b
Regression of stem mass/length vs. age*				
a	1.56	2.15	1.18	1.09
b	0.25	0.44	0.58	0.32
r^2	0.92	0.98	0.98	0.99
Stem secondary growth (%/yr)†	28	56	78	38
Stem secondary growth (g/seedling)	2.0 ± 0.5^a	16.5 ± 6.8^b	14.1 ± 4.6^b	0.4 ± 0.1^a
Apical growth (g/seedling)	4.2 ± 0.7^a	27.9 ± 8.8^b	10.1 ± 2.5^{ab}	0.6 ± 0.2^c
Secondary growth (% aboveground growth)	31.4 ± 5.5^a	32.7 ± 2.3^a	53.3 ± 5.2^b	41.5 ± 2.8^{ab}
Aboveground RGR $(g \cdot g^{-1} \cdot yr^{-1})$‡	0.35 ± 0.02^a	0.62 ± 0.05^b	0.55 ± 0.03^b	0.43 ± 0.02^a
Root : shoot ratio	0.57 ± 0.11^a	0.38 ± 0.03^{ab}	0.24 ± 0.03^b	0.39 ± 0.04^{ab}
Current-leaf N (% of dry mass)§	0.89 ± 0.12^a	1.43 ± 0.09^{ab}	2.11 ± 0.03^b	1.41 ± 0.14^{ab}
Current-leaf P (% of dry mass)§	0.119 ± 0.020^a	0.185 ± 0.008^b	0.295 ± 0.009^c	0.222 ± 0.011^b
Aboveground N (mg/seedling)§	0.16 ± 0.02^a	0.85 ± 0.19^a	0.96 ± 0.25^a	0.07 ± 0.02^a
Aboveground P (mg/seedling)§	0.02 ± 0.004^a	0.12 ± 0.03^a	0.12 ± 0.03^a	0.01 ± 0.003^a
N RAR $(g \cdot g^{-1} \cdot yr^{-1})$§	0.27 ± 0.03^a	0.51 ± 0.04^a	0.33 ± 0.05^a	0.27 ± 0.05^a
P RAR $(g \cdot g^{-1} \cdot yr^{-1})$§	0.29 ± 0.03^a	0.47 ± 0.05^a	0.40 ± 0.05^a	0.28 ± 0.05^a
Sample size (no. seedlings)	3	7	7	17

* $Ln(mg/cm) = a + b(yr)$, $n = 9$ age classes of stem.
† Stem secondary growth $= 100(e^b - 1)$.
‡ Includes secondary stem growth.
§ Sample size for nutrient data = 5 seedlings (3 for pioneer stage).

TABLE 8. Growth and allocation of spruce seedlings transplanted into each major successional stage at Glacier Bay in control plots and in plots manipulated by addition of alder litter, shading, or root trenching. T_0 = initial seedling biomass at time of transplant ($n = 20$ seedlings). Data are means $\pm$ 1 SE, $n = 10$ sites/stage. Statistics as in Table 3. Some treatments were not imposed in certain stages (ND).

Parameter Treatment	Successional stage			
	Pioneer	*Dryas*	Alder	Spruce
Total biomass (g/plant) (T_0 = 4.9 g)				
Control	7.8 ± 0.5^b	8.7 ± 0.5^b	12.4 ± 0.5^c	5.3 ± 0.4^a
Alder litter	$9.2 \pm 0.6^*$	$10.1 \pm 0.5^*$	11.6 ± 0.5	5.1 ± 0.5
Shade	8.0 ± 0.3	8.0 ± 0.3	ND	ND
Trench	ND	ND	$16.5 \pm 1.1^*$	6.5 ± 0.9
Aboveground production $(g \cdot plant^{-1} \cdot yr^{-1})$				
Control	0.19 ± 0.06^a	0.84 ± 0.11^c	1.47 ± 0.15^d	0.46 ± 0.05^b
Alder litter	$0.66 \pm 0.24^*$	$1.44 \pm 0.18^*$	1.44 ± 0.12	0.44 ± 0.08
Shade	0.17 ± 0.02	0.68 ± 0.10	ND	ND
Trench	ND	ND	$2.68 \pm 0.27^*$	$0.88 \pm 0.20^*$
Relative growth rate $(g \cdot g^{-1} \cdot yr^{-1})$				
Control	0.03 ± 0.01^a	0.13 ± 0.01^b	0.15 ± 0.01^c	0.11 ± 0.01^b
Alder litter	$0.08 \pm 0.02^*$	$0.19 \pm 0.02^*$	0.15 ± 0.01	0.10 ± 0.01
Shade	0.03 ± 0.00	0.11 ± 0.01	ND	ND
Trench	ND	ND	$0.21 \pm 0.01^*$	$0.15 \pm 0.01^*$
Root : shoot ratio				
Control	0.28 ± 0.02^a	0.28 ± 0.01^a	0.17 ± 0.01^b	0.18 ± 0.01^b
Alder litter	0.26 ± 0.01	0.25 ± 0.01	0.17 ± 0.01	0.20 ± 0.01
Shade	0.29 ± 0.02	0.27 ± 0.01	ND	ND
Trench	ND	ND	$0.15 \pm 0.00^*$	0.17 ± 0.01
Height increment after 3 yr (cm)				
Control	1.16 ± 0.59^a	2.75 ± 0.30^a	11.08 ± 0.88^b	9.15 ± 1.24^b
Alder litter	1.70 ± 0.40	3.51 ± 0.49	11.63 ± 0.76	8.08 ± 2.65
Shade	2.34 ± 0.70	$4.29 \pm 0.40^*$	ND	ND
Trench	ND	ND	$18.33 \pm 1.35^*$	12.10 ± 2.44

TABLE 9. Survivorship and height growth of spruce and alder seedlings transplanted into control plots of each major successional stage at Glacier Bay. Data are means ± 1 SE, $n = 10$ sites/stage. Values for each time period with the same letter are not significantly different ($P > .05$).

Parameter Species	Year	Successional stage			
		Pioneer	*Dryas*	Alder	Spruce
Survivorship (% of total)					
Spruce	1987	100 ± 0[a]	98 ± 2[a]	100 ± 0[a]	100 ± 0[a]
	1988	100 ± 0[a]	97 ± 3[a]	100 ± 0[a]	96 ± 3[a]
	1989	100 ± 0[a]	97 ± 3[a]	100 ± 0[a]	90 ± 5[a]
Alder	1987	89 ± 4[a]	77 ± 6[a]	81 ± 5[a]	70 ± 6[a]
	1988	86 ± 6[a]	68 ± 9[ab]	63 ± 10[ab]	51 ± 7[b]
	1989	86 ± 6[a]	58 ± 10[ab]	43 ± 10[b]	44 ± 7[b]
Height growth (cm)		***	**	***	*
Spruce	1987	1.83 ± 0.13[b]	1.43 ± 0.12[a]	3.28 ± 0.13[c]	3.73 ± 0.33[c]
	1988	0.94 ± 0.06[a]	1.04 ± 0.10[a]	4.13 ± 0.26[b]	4.23 ± 0.27[b]
	1989	0.24 ± 0.09[a]	0.85 ± 0.17[b]	5.45 ± 0.52[d]	4.21 ± 0.18[c]
	1987–1989	1.16 ± 0.59[a]	2.75 ± 0.30[b]	11.08 ± 0.88[b]	9.15 ± 1.24[b]
		*			
Alder	1987	5.76 ± 0.67[a]	1.24 ± 0.09[c]	3.27 ± 0.43[b]	3.46 ± 0.72[b]
	1988	11.61 ± 1.40[a]	4.50 ± 0.37[b]	4.39 ± 0.38[b]	5.24 ± 0.80[b]
	1989	15.51 ± 2.80[a]	1.95 ± 0.74[c]	2.56 ± 0.51[b]	3.24 ± 0.56[b]
	1987–1989	26.55 ± 3.37[a]	−16.96 ± 5.59[c]	4.24 ± 2.64[b]	2.60 ± 2.10[b]

$* P < .05; ** P < .01; *** P < .001$ (slope of linear regression differs significantly from 0, indicating significant change in height growth with time).

trient content and/or relative accumulation rate increased with addition of alder litter in the pioneer and *Dryas* stages (Table 11). Tissue nutrient concentrations were relatively unaffected by addition of alder litter in the pioneer and *Dryas* stages because seedling growth diluted the nutrients accumulated by seedlings (Table 10). Thus, nutrients released from alder litter stimulate nutrient accumulation and growth in the pioneer and *Dryas* stages but not in later successional stages.

Shading increased height growth and needle nutrient concentrations of spruce in the *Dryas* stage (an etiolation response) but otherwise had no effect on any measured parameter (Tables 8 and 10).

Planting spruce seedlings near isolated alders in the pioneer stage increased tissue N concentration (Table 10) but had no detectable effect on growth of spruce seedlings (data not shown), indicating that any facilitative effect of alder on seedling growth requires a substantial density of alder.

Elimination of root competition by woody species caused an increase in aboveground production, RGR, tissue N and P concentration, seedling N and P content, and seedling relative nutrient accumulation rates (RAR) in the alder and spruce stages, and an increase in seedling biomass and 3-yr height increment in the alder stage (Tables 8, 10, and 11). The fact that this trenching treatment had progressively greater effect on height growth through time (data not shown) indicates that the plants were responding to long-term changes in resource availability in the trenched plots due to reduced root competition, not just a pulse of nutrient input from death of fine roots in the year after trench-

TABLE 10. Nitrogen and phosphorus concentration of current-year's needles of spruce seedlings transplanted into each major successional stage at Glacier Bay. Data are means ± 1 SE, $n = 5$ sites/stage. Statistics as in Table 3; treatments as in Table 8.

Nutrient Treatment	Successional stage			
	Pioneer	*Dryas*	Alder	Spruce
Nitrogen (% dry mass)				
Control	0.48 ± 0.02[a]	0.81 ± 0.06[b]	1.71 ± 0.22[d]	1.26 ± 0.09[c]
Alder litter	0.48 ± 0.07	1.08 ± 0.06*	1.91 ± 0.12	1.41 ± 0.12
Shade	0.74 ± 0.03	1.25 ± 0.11*	ND	ND
Trench	ND	ND	2.45 ± 0.19*	2.15 ± 0.08*
Near alder	1.14 ± 0.21*	1.03 ± 0.06	ND	ND
Far from alder	0.58 ± 0.05	0.81 ± 0.06	ND	ND
Phosphorus (% dry mass)				
Control	0.141 ± 0.006[a]	0.176 ± 0.010[a]	0.233 ± 0.019[b]	0.233 ± 0.009[b]
Alder litter	0.155 ± 0.009	0.182 ± 0.003	0.248 ± 0.010	0.240 ± 0.010
Shade	0.169 ± 0.005	0.235 ± 0.016*	ND	ND
Trench	ND	ND	0.287 ± 0.012*	0.320 ± 0.018*
Near alder	0.158 ± 0.013	0.158 ± 0.005	ND	ND
Far from alder	0.128 ± 0.013	0.176 ± 0.010	ND	ND

ing. Root : shoot ratio was not significantly affected by our manipulations in any stage. We conclude that the extremely slow growth in the pioneer and *Dryas* stages is largely due to low nutrient availability and that root competition for some soil resource reduces nutrient status and growth in the alder and spruce stages.

Alder.—Seedling transplants of alder had 10-fold higher biomass, 6-fold greater total height increment, 3-fold higher growth rate, and a trend toward greater survivorship in the pioneer stage than in later successional stages (Fig. 10, Tables 9 and 12). Alder transplants showed no significant change in seedling biomass over the 3-yr growth experiment in any of the vegetated successional stages (Table 12). This probably reflected the sensitivity of alder to drought in the sandy *Dryas* soils and to shade in the alder and spruce stages. Alder seedlings lost height in the *Dryas* stage (Table 9), due to frequent death of the main shoot and resprouting from the base.

As with biomass, there were large increases in N and P pools of alder seedlings transplanted into the pioneer stage, but no increase in nutrient pools of seedlings transplanted into other successional stages (Fig. 11, Table 13).

Addition of alder litter had no significant effect on any measured parameter in any stage (except a reduction in RGR in the alder stage; one significant effect out of 44 comparisons; Tables 12–14), confirming that environmental conditions other than nutrient supply were responsible for slow growth and reduced survivorship of alder in the *Dryas*, alder, and spruce stages. Shading (66% reduction in irradiance) decreased alder biomass, aboveground production, RGR, and seedling
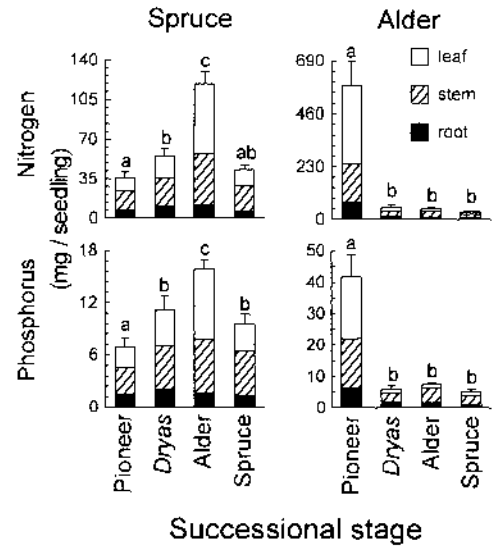

Fig. 11. Nitrogen and phosphorus pools in roots, stems, and leaves of control spruce and alder seedlings transplanted into four successional stages. Data are means (and 1 SE of total seedling nutrient pool), $n = 5$ sites per stage. Means of total seedling pool with the same letter are not significantly different ($P > .05$).

N and P contents in the pioneer stage but had no effect on height growth, indicating that alder growth is more light sensitive than spruce, but shows a similar etiolation response to the reduction in light. In the *Dryas* stage, shading stimulated RGR (Table 12) and 3rd-yr height growth (data not shown), suggesting that the reduction in light may have ameliorated the drought conditions in this stage. Trenching caused increased

TABLE 11. Nitrogen and phosphorus content and relative accumulation rate (RAR) of N and P in spruce seedlings transplanted into the four major successional stages at Glacier Bay. $T_0 =$ initial seedling biomass at time of transplant. Data are means $\pm$ 1 SE, $n = 10$ sites/stage. Statistics as in Table 3; treatments as in Table 8.

Parameter	Successional stage			
Treatment	Pioneer	*Dryas*	Alder	Spruce
Seedling N content (mg/plant) ($T_0 = 54.3$)				
Control	35.6 ± 5.4[a]	54.8 ± 7.1[b]	118.6 ± 11.4[c]	43.4 ± 4.1[ab]
Alder litter	41.3 ± 6.3	69.9 ± 5.9*	87.6 ± 4.4*	34.2 ± 3.7*
Shade	42.5 ± 4.9	43.4 ± 2.9	ND	ND
Trench	ND	ND	185.8 ± 13.2*	64.4 ± 13.2*
N RAR (mg·mg⁻¹·yr⁻¹)				
Control	0.04 ± 0.01[a]	0.18 ± 0.02[b]	0.27 ± 0.02[c]	0.15 ± 0.02[b]
Alder litter	0.10 ± 0.03*	0.30 ± 0.04*	0.40 ± 0.02*	0.20 ± 0.02*
Shade	0.04 ± 0.01	0.25 ± 0.04	ND	ND
Trench	ND	ND	0.43 ± 0.02*	0.32 ± 0.03*
Seedling P content (mg/plant) ($T_0 = 9.8$)				
Control	6.87 ± 1.10[a]	11.10 ± 1.73[b]	15.85 ± 1.13[c]	9.57 ± 1.13[b]
Alder litter	8.21 ± 1.18	13.67 ± 1.25	13.68 ± 0.73	7.49 ± 1.06
Shade	8.00 ± 1.02	8.69 ± 0.46	ND	ND
Trench	ND	ND	26.20 ± 2.07*	13.53 ± 2.83
P RAR (mg·mg⁻¹·yr⁻¹)				
Control	0.05 ± 0.01[a]	0.20 ± 0.03[bc]	0.27 ± 0.03[c]	0.16 ± 0.02[b]
Alder litter	0.13 ± 0.03*	0.27 ± 0.03	0.34 ± 0.01*	0.19 ± 0.02
Shade	0.05 ± 0.01	0.23 ± 0.03	ND	ND
Trench	ND	ND	0.42 ± 0.02*	0.26 ± 0.02*

TABLE 12. Growth and allocation of alder seedlings transplanted into each major successional stage at Glacier Bay. T_0 = initial seedling biomass at time of transplant. Data are means ± 1 SE, n = 10 sites/stage. Statistics as in Table 3; treatments as in Table 8.

Parameter Treatment	Successional stage			
	Pioneer	*Dryas*	Alder	Spruce
Total biomass (g/plant) (T_0 = 2.4 g)				
Control	36.8 ± 6.0ᵃ	3.4 ± 0.9ᵇ	3.2 ± 0.3ᵇ	3.0 ± 0.4ᵇ
Alder litter	38.9 ± 6.4	2.9 ± 0.5	3.2 ± 0.4	2.6 ± 0.3
Shade	17.2 ± 2.6*	3.9 ± 0.5	ND	ND
Trench	ND	ND	3.8 ± 0.6	3.6 ± 0.8
Aboveground production (g·plant⁻¹·yr⁻¹)				
Control	17.6 ± 3.5ᵃ	0.7 ± 0.4ᵇ	0.5 ± 0.1ᵇ	0.4 ± 0.1ᵇ
Alder litter	18.1 ± 3.7	0.5 ± 0.3	0.3 ± 0.1	0.4 ± 0.1
Shade	6.7 ± 1.6*	0.9 ± 0.2	ND	ND
Trench	ND	ND	0.8 ± 0.2*	0.9 ± 0.2*
Relative growth rate (g·g⁻¹·yr⁻¹)				
Control	0.57 ± 0.09ᵃ	0.27 ± 0.07ᵇ	0.21 ± 0.02ᵇ	0.21 ± 0.04ᵇ
Alder litter	0.81 ± 0.05	0.29 ± 0.07	0.15 ± 0.03*	0.22 ± 0.03
Shade	0.59 ± 0.06*	0.42 ± 0.06*	ND	ND
Trench	ND	ND	0.31 ± 0.03*	0.32 ± 0.03
Root:shoot ratio				
Control	0.43 ± 0.04ᵇ	1.49 ± 0.35ᵃ	0.34 ± 0.03ᶜ	0.26 ± 0.03ᶜ
Alder litter	0.40 ± 0.04	1.31 ± 0.30	0.36 ± 0.05	0.34 ± 0.02
Shade	0.44 ± 0.04	1.20 ± 0.33	ND	ND
Trench	ND	ND	0.30 ± 0.07*	0.27 ± 0.03
Height increment after 3 yr (cm)				
Control	26.6 ± 3.4ᵇ	−17.0 ± 5.6ᵃ	4.2 ± 2.6ᶜ	2.6 ± 2.1ᶜ
Alder litter	30.8 ± 4.1	−19.9 ± 4.2	2.1 ± 3.4	5.2 ± 2.1
Shade	26.4 ± 3.4	−12.0 ± 4.9	ND	ND
Trench	ND	ND	9.2 ± 5.0	6.2 ± 4.3

aboveground production, RGR (alder stage only), and N accumulation of alder in the alder and spruce stages, indicating that alder was sensitive to root competition as well as shading in these later successional stages. Our manipulations had no effect on survivorship of either spruce or alder (data not shown).
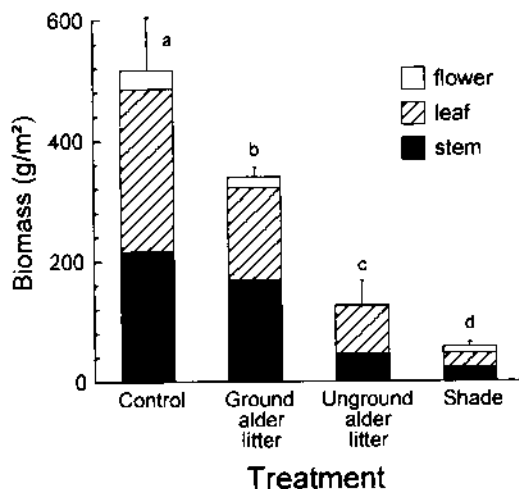

FIG. 12. Effect of ground and unground alder litter and of shading on aboveground biomass of *Dryas*. Data are means (and 1 SE of total aboveground biomass), n = 10 sites/stage. Means of total biomass with the same letter are not significantly different (P > .05).

Alder effects on Dryas

Aboveground biomass of *Dryas* was reduced 16-fold by a 66% reduction in irradiance (Fig. 12). Unground alder litter, which had both a shading and a chemical effect, reduced *Dryas* biomass 4-fold, and addition of ground alder litter, which had a chemical effect but negligible shading effect, reduced *Dryas* biomass 30%. Thus, alder inhibited growth of *Dryas* primarily by shading, but the chemical effects of alder litter were also inhibitory, despite the strong nutrient limitation of spruce seedling growth at this site.

DISCUSSION

Overview

Our study demonstrates that facilitation is only one of several important mechanisms causing successional change at this site. Plant life history traits associated with dispersal ability are critical to early-successional dynamics at Glacier Bay, where 100 km of linear glacial retreat during the past two centuries resulted in newly exposed terrain becoming progressively remote from seed sources. Both long-distance seed dispersal and short generation time are prerequisites for plants reaching early-successional communities including our pioneer and *Dryas* stages.

Succession from *Dryas* to the alder stage involves competitive displacement as tall shrubs shade out

TABLE 13. Nitrogen and phosphorus content and relative accumulation rate (RAR) of N and P in alder seedlings transplanted into the four major successional stages at Glacier Bay. T_0 = initial seedling biomass at time of transplant. Data are means ± 1 SE, n = 10 sites/stage. Statistics as in Table 3; treatments as in Table 8.

| Parameter | Successional stage | | | |
Treatment	Pioneer	Dryas	Alder	Spruce
Seedling N content (mg/plant)				
Control (T_0 = 49)	585 ± 102[a]	52 ± 14[b]	47 ± 5[b]	32 ± 5[b]
Alder litter	609 ± 108	43 ± 9	45 ± 8	42 ± 12
Shade	267 ± 54*	61 ± 9	ND	ND
Trench	ND	ND	57 ± 10	54 ± 10
N RAR (mg·mg⁻¹·yr⁻¹)				
Control	1.60 ± 0.13[a]	0.50 ± 0.13[b]	0.41 ± 0.06[b]	0.42 ± 0.09[b]
Alder litter	1.66 ± 0.07	0.39 ± 0.12	0.33 ± 0.04	0.44 ± 0.08
Shade	1.40 ± 0.12	0.76 ± 0.10	ND	ND
Trench	ND	ND	0.78 ± 0.10*	0.72 ± 0.07*
Seedling P content (mg/plant)				
Control (T_0 = 9.0)	41.8 ± 7.2[a]	5.9 ± 1.2[b]	7.4 ± 0.9[b]	5.2 ± 0.8[b]
Alder litter	39.6 ± 7.5	5.7 ± 0.8	7.0 ± 1.2	7.5 ± 1.8
Shade	16.0 ± 4.1*	7.6 ± 1.2	ND	ND
Trench	ND	ND	8.2 ± 1.4	9.0 ± 1.5
P RAR (mg·mg⁻¹·yr⁻¹)				
Control	1.14 ± 0.13[a]	0.42 ± 0.11[b]	0.30 ± 0.05[b]	0.41 ± 0.07[b]
Alder litter	1.43 ± 0.10	0.32 ± 0.10	0.22 ± 0.03	0.30 ± 0.05
Shade	1.36 ± 0.14	0.52 ± 0.08	ND	ND
Trench	ND	ND	0.46 ± 0.05	0.57 ± 0.05

shorter plants (*Dryas, Epilobium,* etc.) and produce an environment that benefits potential herbivores and pathogens of understory plants. Similarly, because the height at maturity of spruce is greater than that of alder, spruce eventually outcompetes alder. In both cases, final size and longevity are major factors causing successional change.

The basic pattern of succession to taller plants occurs despite the strong net inhibitory effect (nearly 100%) of *Dryas* and alder on initial establishment of their successors (alder and spruce, respectively). Thus, if mid- and late-successional species do not disperse to new sites before initial colonizers modify the microenvironment for seedling establishment, invasion will be slowed or prevented by initial vegetation (Egler 1954). For those spruce seedlings that established prior to

arrival of the dense alder thicket, the net effect of the alder stage is facilitative, despite competitive impact on spruce through preemption of light and soil resources. Thus, life history traits, competitive inhibition, and facilitation are all essential in explaining successional change at Glacier Bay, as concluded in other postglacial successional seres (Burrows 1990, Matthews 1992).

Successional change in environment

The successional changes in environment that we observed at Glacier Bay were similar to patterns observed previously, suggesting that our results should be applicable to concepts developed earlier at Glacier Bay. The successional increase in soil organic matter

TABLE 14. Nitrogen and phosphorus concentration of current-year's leaves of alder seedlings transplanted into each major successional stage at Glacier Bay. Data are means ± 1 SE, n = 5 sites/stage. Statistics as in Table 3; treatments as in Table 8.

| Nutrient | Successional stage | | | |
Treatment	Pioneer	Dryas	Alder	Spruce
Nitrogen (% dry mass)				
Control	2.65 ± 0.12[a]	2.85 ± 0.14[a]	2.93 ± 0.20[a]	2.34 ± 0.23[a]
Alder litter	2.72 ± 0.05	3.18 ± 0.37	3.04 ± 0.09	2.47 ± 0.18
Shade	2.86 ± 0.18	3.12 ± 0.08	ND	ND
Trench	ND	ND	3.28 ± 0.15	3.20 ± 0.20*
Phosphorus (% dry mass)				
Control	0.153 ± 0.003[a]	0.245 ± 0.038[ab]	0.267 ± 0.034[ab]	0.361 ± 0.060[b]
Alder litter	0.135 ± 0.005	0.246 ± 0.030	0.279 ± 0.022	0.317 ± 0.021
Shade	0.137 ± 0.016	0.232 ± 0.025	ND	ND
Trench	ND	ND	0.288 ± 0.025	0.414 ± 0.040

STAGE:	Pioneer	*Dryas*	Alder	Spruce

FACILITATIVE EFFECTS:

Pioneer: ↑ Survivorship

Dryas: ↑ N (weak) ↑ Growth (weak)

Alder: ↑ SOM ↑ N ↑ Mycorrhizae ↑ Growth

Spruce: ↑ Germination

INHIBITORY EFFECTS:

Pioneer: ↓ Germination (weak)

Dryas: ↓ Germination ↓ Survivorship ↑ Seed predation and mortality

Alder: ↓ Germination ↓ Survivorship ↑ Seed predation and mortality Root competition Light competition

Spruce: ↓ Growth ↓ Survivorship ↑ Seed predation and mortality Root competition Light competition ↓ N
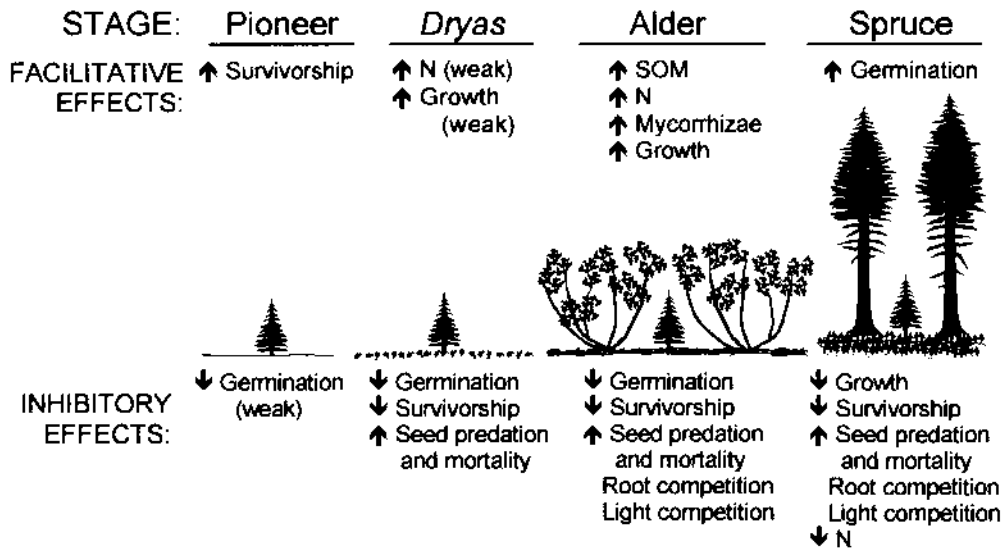
FIG. 13. Summary of facilitative and inhibitory effects (weak effects noted) of each successional stage on establishment and growth of spruce seedlings at Glacier Bay, as determined from field observations, field experiments, and greenhouse studies.

content and associated decline in pH and bulk density and increase in soil moisture and total N that we observed are typical of succession following deglaciation (Crocker and Major 1955, Crocker and Dickson 1957, Ugolini 1966, 1968, Viereck 1966, Jacobson and Birks 1980, Sondheim and Standish 1983, Messer 1988, Bormann and Sidle 1990, Matthews 1992) and of nonglacial primary successional seres (Van Cleve et al. 1971, 1991, Vitousek et al. 1983, Walker 1989). However, the large amount and variable distribution of rock and pore space in Glacier Bay till (≈75% of the soil volume) complicates estimations of soil nutrient pools in the field. Crocker and Major (1955) explicitly selected relatively uncommon sites with few rocks so they could sample with a soil corer. By contrast, we, F. C. Ugolini (1966, *personal communication*), and Bormann and Sidle (1990) chose sites randomly with respect to rockiness. As a result of this difference in methodology and differences in profile depth, our estimate of soil pool sizes and rates of N accumulation in mineral soil during the alder stage of succession ($0.83 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) are similar to those of Ugolini (1968; $0.81 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and Bormann and Sidle (1990; $1.1 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) but less than that of Crocker and Major ($2.6 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). The often-cited N accumulation rate of Crocker and Major (1955; $4.9 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for the mineral plus organic horizons) is among the highest reported for any successional sere and probably reflects an overestimate of the soil nutrient pools that are representative of each site.

Our study provides several lines of evidence that N availability increases from the pioneer to the alder stage: increases in tissue nutrient concentrations, nutrient pools, and N accumulation rates of transplanted spruce seedlings, N concentration of naturally occurring seedlings, annual N flux in litterfall, seedling growth in greenhouse bioassays of soils (a nonsignificant trend), and rate of N accumulation in soils. In all these indices of N availability (except the greenhouse bioassay), alder had a greater facilitative effect on N availability than did *Dryas*. Similarly, Crocker and Major (1955) observed that soil N accumulated most rapidly beneath alder and that N accumulation rates were similar beneath willow, poplar (non-N-fixers), and the N-fixing *Dryas*. In other postglacial successional seres, *Dryas* is not nodulated and also contributes relatively little to N accumulation (Fitter and Parsons 1987, Blundon and Dale 1990). Thus, at Glacier Bay all vegetation enhances soil N supply, but this effect is most pronounced with alder (Fig. 13).

The decline from the alder to spruce stage in available ammonium, nitrate, exchangeable cations, and phosphate, in net primary production (Bormann and Sidle 1990), and in spruce growth rate, needle N concentration, seedling N content, and N and P accumulation rate (this study) all suggest a decline in nutrient availability in late succession at Glacier Bay (Fig. 13). Similarly, in primary succession on river floodplains in interior Alaska, nutrient availability is highest in mid-successional deciduous forests and declines in the late-successional white spruce forest (Walker 1989, Van Cleve et al. 1991). These patterns conflict with the generalization that nutrient availability increases monotonically through primary succession (Tilman 1985, 1988). Matthews (1992) reviewed nutrient availability in other glacial forelands and noted that most studies show increasing or stable N values through time. A broad comparison of N levels in five classes of primary succession (Walker 1993) showed that the general pattern is a rapid increase in total N during the first

50–200 yr followed by an asymptote reached after 200–2000 yr. Certain seres (e.g., dunes) are slower to reach the asymptote than others (e.g., floodplains), and the wide variation in N accumulation rates appears poorly related to the presence or absence of N-fixing vascular plants (Walker 1993) and may reflect differences in parent material, topography, or climate (Jenny 1980, Matthews 1992). Nonetheless, in long successional seres, chemical and biological processes tend to bind nutrients in unavailable form in late succession in soil minerals (Walker and Syers 1976), dead soil organic matter (Van Cleve et al. 1991, Vitousek and Howarth 1991), and vegetation (Crocker and Major 1955), leading to the general decline in productivity of late-successional vegetation postulated by Odum (1969).

The decline in total soil P that we observed from the alder to the spruce stage parallels declines in available P (Bormann and Sidle 1990) and could reflect transfer to overlying vegetation and soil organic mat (Crocker and Major 1955), occlusion in some form resistant to acid digestion (Walker and Syers 1976), or leaching loss. Several studies (but see Jacobson and Birks 1980) of soil P in postglacial succession also show declining values over time (Matthews 1992).

The sandier soils from our *Dryas* stage compared to other stages complicate interpretations about the impact of the *Dryas* community on the establishment and growth of later successional species. *Dryas* spp. commonly dominate dry, alkaline ridges and fellfields (Cooper 1923*b*, Lawrence et al. 1967). Nonetheless, scattered alders, cottonwoods, and spruce were growing in our *Dryas* sites, as had been observed in our alder sites when they were dominated by *Dryas* (Crocker and Major 1955, Lawrence et al. 1967), suggesting that these sites would eventually proceed through alder and spruce successional stages. Thus, results from our *Dryas* sites should be treated with caution but are probably not atypical of this stage of succession.

The successional decline in understory light availability, although not documented previously at Glacier Bay, is typical of most plant successional sequences and leads to a decreasing ratio of available aboveground to belowground resources (Tilman 1985). Root : shoot ratio was higher in the pioneer and *Dryas* stages than in the alder or spruce stages for spruce germinants from sown seed, naturally occurring spruce seedlings, and spruce transplants, demonstrating that nutrients were most limiting early in succession. However, there were no consistent changes in root : shoot ratio from the alder to the spruce stage.

Seed rain and initial establishment

The order in which species colonize at Glacier Bay correlates closely with dispersability (Cooper 1931). Our seed-rain and seed-sowing experiments show that the low density of naturally occurring alders and spruce in the pioneer stage reflect low seed rain rather than inability of young seedlings to germinate, grow, and

survive. Spruce, and to a lesser extent alder, are slow to arrive on recently deglaciated terrain because they have heavier seeds and a greater age to first reproduction than initial colonizers like willow and *Dryas* (Cooper 1923*b*, Lawrence 1958, Drury and Nisbet 1973), a pattern typical of primary successional seres (Matthews 1992, Chapin 1993, del Moral and Wood 1993) other than islands (Rydin and Borgegård 1991). For the same reasons, alder seeds arrive in greater abundance in the *Dryas* stage than do spruce seeds in the alder stage. Alder may require the winds associated with open terrain for effective dispersal because there was no detectable alder seed rain in the spruce stage, even though alders were abundant along nearby streams and were scattered through the forest. Thus, the *pattern* of succession at Glacier Bay is adequately explained by life history traits without invoking biotic interactions among species, as observed previously for Glacier Bay (Matthews 1992) and other successional seres (Noble and Slatyer 1980, Walker et al. 1986, Adams and Dale 1987). In alpine primary succession, dispersal distances may be short enough that seed rain is less important in explaining successional change (Matthews 1992, but see del Moral and Wood 1993).

Vegetation in each successional stage inhibited initial germination and establishment of alder and spruce (Fig. 13). In the pioneer stage, the "black-crust" algal/microbial community had mixed effects, tending to reduce germination but promote survivorship of alder and spruce seedlings. The two subsequent stages (*Dryas* and alder) each inhibited spruce germination more strongly than the previous stage. Alder germination was completely prevented by all stages other than the pioneer stage. The high percentage germination of both spruce and alder in the pioneer stage reflects a requirement of these genera for a mineral-soil seedbed (Walker et al. 1986).

Even on a mineral-soil seedbed, the *Dryas* and alder stages inhibited germination and survivorship, perhaps due to indirect biotic effects (Connell 1990). These effects could include seed/seedling predation by birds and microtines, which increase in abundance from early to mid-succession (Good 1966, Trautman 1966), and attacks by seed/seedling pathogens, which are more abundant (Sprague and Lawrence 1960) and may be more effective in the constantly humid environment of alder thickets or spruce forests than in early succession. The fact that interstage differences in germination on mineral soils were more pronounced in the field than in the greenhouse supports the idea that complex biotic mechanisms operate in the field by which each stage "inhibits" germination of later successional species (Connell 1990). The inhibitory effect of spruce soils on spruce germination, of alder soils on alder germination, and of alder litter on germination of both species in the greenhouse suggest that allelopathic effects may also be involved. The critical point is that, at this initial stage of the life cycle, each successional stage

has an inhibitory rather than a facilitative effect, consistent with previous observations in riparian primary succession (Walker and Chapin 1986). Unless spruce establishes before there is a well-developed vegetation cover of *Dryas* or alder, the facilitative effect of *Dryas* or alder on growth of established spruce seedlings may be a moot point (Cooper 1931).

Plant growth and nutrient uptake

Spruce. — Our observations of naturally occurring seedlings and of seedling transplants of known history indicate that each successional stage had both facilitative and inhibitory effects on growth of later successional species (Fig. 13). The slow growth of naturally occurring spruce seedlings in the pioneer stage is consistent with previous observations (Cooper 1923*b*, Lawrence 1958) and was matched by slow growth of spruces transplanted to the field. The stimulation of spruce growth in pioneer and *Dryas* stages by addition of alder litter in the field and the greater growth of spruce seedlings in alder or *Dryas* soils than in pioneer soils in the greenhouse shows that something associated with low quantities of soil organic matter is partially responsible for the slow growth of spruce in the pioneer stage. Cooper (1923*b*, 1931), who was unaware of the N-fixing capability of alder, ascribed the facilitative effect of alder humus to general moisture and nutrient amelioration and observed that spruce seedlings grew more rapidly when associated with either willows or alder than on bare soil in the pioneer stage. Lawrence (1951) ascribed this facilitative effect to N fixation by alder because his fertilizer experiments showed that N was the primary nutrient limiting cottonwood growth in the pioneer stage and that alder leaves and duff were as effective as N (but less effective than a complete fertilizer) in stimulating cottonwood growth. Similarly, cottonwood seedlings associated with *Dryas* or alder grew faster than those growing in unvegetated soils (Lawrence 1958, Schoenike 1958, Lawrence et al. 1967). Our greenhouse studies demonstrate that low availability of N and P by themselves could not explain slow growth of spruce in pioneer soils. Spruce growth was stimulated more by nutrient addition in soils from the spruce and alder stages than in soils from the pioneer stage.

Stimulation of spruce growth by alder or *Dryas* may not be a simple consequence of N fixation. When spruce seedlings were transplanted to the pioneer stage, they lost ectomycorrhizal mantles originally present at the time of transplant (M. E. Gutierrez and F. S. Chapin, III, *unpublished manuscript*). These pioneer soils typically lack mycorrhizal fungi (Sprague and Lawrence 1960). Growth chamber experiments showed that both low pH and microbial innoculum were essential for spruce growth on pioneer soils (M. E. Gutierrez and F. S. Chapin, III, *unpublished manuscript*), perhaps because these ectomycorrhizae require moderate/low pH. Thus, alder may facilitate spruce growth by con-

tributing organic matter that reduces pH (Crocker and Major 1955), allowing mycorrhizal colonization, as well as by directly increasing soil N availability. This is consistent with our observation that improved growth of spruce seedlings in the *Dryas* and alder stages was associated with increased tissue concentrations of both P and N. If alder affected only N nutrition, the increased growth would have reduced tissue P concentration by dilution rather than increasing it, as we observed. Thus, alder improves nutritional conditions relative to those present in the pioneer stage through more than simple N fixation.

The net facilitative effect of the *Dryas* stage on spruce growth (nonsignificant trend) and nutrient uptake relative to the pioneer stage presumably reflects both the N-fixing capability of *Dryas* (Lawrence et al. 1967) and the trend toward greater soil organic matter and N accumulation. However, addition of alder litter stimulated spruce growth and nutrient uptake to about the same degree in the *Dryas* as in the pioneer site, indicating that, even in the *Dryas* site, spruce growth was strongly nutrient limited. This is consistent with the observation (Table 1; Crocker and Major 1955) that N accumulates quite slowly beneath *Dryas* mats (cf. Crocker and Major 1955, Fitter and Parsons 1987, Blundon and Dale 1990).

The strong facilitative effect of the alder stage on growth of transplanted spruce seedlings relative to both the pioneer and *Dryas* stages reflects the large annual input of N through fixation and litterfall (Table 2; Crocker and Major 1955, Lawrence 1958). Seedlings of spruce (Fig. 10) and cottonwood (Lawrence 1951, 1958), but not alder (Fig. 10) in the alder stage were facilitated relative to the pioneer stage. Although the net effect of the alder stage on spruce growth was positive, the root-trenching experiments showed that alders also competed with understory spruce seedlings for soil resources. The magnitude of competitive release from root-trenching was as great as the difference in growth of control transplants between the *Dryas* and alder stages. Moreover, when the alder canopy was tied back to expose understory spruces to higher light intensity without disturbing roots, there was a substantial increase in ring width (C. L. Fastie, *personal observations*). Naturally occurring spruce saplings greatly increase their ring width at the time they emerge above the alder canopy (C. L. Fastie, *personal observations*). Together these observations indicate that, although alder has a net positive effect on established spruce seedlings, it also competes strongly with understory spruce seedlings. Thus, the major facilitative effect of alder may occur after spruce emerges above the alder canopy.

Contrary to our expectation, spruce seedlings planted beneath the canopy of isolated alders in the pioneer and *Dryas* stages, where they had substantial light as well as input of alder litter, grew no better than control seedlings planted far from alders. Since spruce clearly responded to experimental addition of alder litter with-

in the 3-yr time frame of our experiment and had higher tissue N concentrations than spruces planted far from alders, competition between these isolated alders and spruce seedlings probably offset the facilitative impact of natural alder litter.

The spruce stage inhibited growth and nutrient uptake of spruce seedlings relative to previous successional stages, probably due to both shading and low nutrient availability, as N and P become bound in living and dead organic matter (Crocker and Major 1955, Van Cleve et al. 1991). The root-trenching experiments demonstrated competition between trees and seedlings for soil resources. In the spruce forest, seedlings were rooted largely in the soil organic horizon, rather than in mineral soil, which the greenhouse experiments showed to be relatively favorable for plant growth. Moreover, if the spruce soil inhibits germination and initial establishment of spruce seedlings, as we observed in the greenhouse, it may also inhibit establishment of spruce seedlings in the field through allelopathic or pathogenic effects. These transplant experiments support tree ring data, indicating that few spruce trees are recruited after a mature spruce forest is formed (C. L. Fastie, *personal observations*).

A key assumption of most successional studies is that vegetation differences among sites of different ages at one point in time are analogous to chronological changes at a given site. When we repeated Lawrence's (1951) alder-litter addition experiments in the same site 35 yr later (after transition from pioneer to alder stage), we no longer saw the stimulatory effect of alder litter that he had observed, clearly demonstrating the facilitative effect of chronological successional change at that site. We also observed that alder litter stimulated spruce growth in the pioneer stage, just as Lawrence (1951) had observed with cottonwood. This confirms that comparison among spatially distinct stages adequately represented the true chronosequence with respect to facilitative impact of intervening *Dryas* and alder stages.

Alder. — In contrast to spruce, growth of alder transplants was inhibited by all except the pioneer stage. In fact, only in the pioneer stage did the alder transplants show any net gain in mass or nutrients over the 3-yr study. Effective growth of alder in the pioneer stage is consistent with observations of naturally occurring seedlings (Cooper 1923b) and is typical of this'and other N-fixing species in high-light, low-N environments (Vitousek and Howarth 1991, Chapin 1993). The strong sensitivity of alder transplants to shading in the pioneer stage probably explains why the alder and spruce stages inhibited growth of alder seedlings. The release of alder seedlings in the root-trenched plots of the alder and spruce stages showed that root competition also contributed to their poor growth in these stages. The reasons for poor growth of alder transplants in the *Dryas* stage are less clear, but may reflect the sandier, drier soils in these sites. Alder requires high

water availability, and this was the only stage where shading had a positive effect on alder relative growth rate.

Dryas. —Our experiments showed that the rapid disappearance of *Dryas* following invasion by alder was due to a combination of shade intolerance (Cooper 1931, Lawrence et al. 1967), physical burial by alder litter, and allelopathic effects of alder litter. Shade intolerance is typical of N-fixing species such as *Dryas* and alder, but the allelopathic effects of alder litter on *Dryas* were unanticipated. *Dryas* is not stimulated by (and may even respond negatively to) addition of commercial fertilizers (Lawrence et al. 1967), suggesting that it is extremely sensitive to its physical and chemical environment.

CONCLUSIONS

This study indicates that, just as in secondary succession, no single factor or mechanism fully accounts for primary succession at Glacier Bay. The pattern of succession is adequately explained by life history traits such as seed size, growth rate, age at first reproduction, maximum height, and longevity. If there were no species interactions, observed life history traits could only produce a progression in dominance from *Dryas* to alder to spruce. If there were no competitive interactions among species, late-successional vegetation would develop more quickly, and *Dryas* and alder might disappear more slowly from the understory, but the predominant physiognomy of each successional stage would not be greatly altered. If there were no facilitation by addition of soil N and organic matter, communities would develop extremely slowly, and the observed productivity and species composition of late-successional vegetation might never be achieved, although nearby successional seres lacking alder also succeed to Sitka spruce (Jacobson and Birks 1980). Thus, life history traits, competitive interactions, and facilitation are all critical causes of successional change at Glacier Bay, and search for a single predominant mechanism seems futile (Finegan 1984, Pickett et al. 1987a, Walker and Chapin 1987).

The relative importance of mechanisms and processes differs among primary successional seres (e.g., Matthews 1992). In contrast to the succession that we described in the east arm of Glacier Bay, succession in the west arm occurs more slowly, with willow thickets dominating most sites and alder largely absent (F. S. Chapin, III et al., *personal observations*). However, even here, succession proceeds through a shrub stage to a stage dominated by Sitka spruce. The differences in succession between these two adjacent postglacial landscapes could reflect wind patterns affecting seed dispersal (Cooper 1931, Lawrence 1979, Matthews 1992), the drier climate of the west arm (Streveler and Paige 1971), greater prominence of bedrock, or other factors. In contrast to the succession under conditions of relatively moderate climate and high-resource parent ma-

terial in the east arm of Glacier Bay, succession in colder or more nutrient-poor sites such as tundra may be driven more by facilitative interactions and less by competition (Walker and Chapin 1987). In the least favorable habitats (e.g., polar deserts or volcanic pumice), primary succession may be limited by direct climatic effects on plant growth rather than by nutrients (Jacobson and Birks 1980, Wood and Morris 1990) or may not occur at all (Svoboda and Henry 1987, Matthews 1992). Thus, generalizations about the importance of facilitation and other successional mechanisms must be placed in a context of resource availability and environmental severity.

Although many factors influence succession at Glacier Bay and elsewhere, their relative importance changes through succession in a predictable fashion. Not surprisingly, in most successional sequences, life history traits promote abundant early arrival and rapid establishment of colonists and greater height and longevity of late-successional species. In primary succession, early arrival is achieved by production of small wind-dispersed seeds, whereas in secondary succession a buried seed bank is more important (Bazzaz 1979, Noble and Slatyer 1987). Most early colonists begin reproduction at a young age and have a high maximum RGR (Grime and Hunt 1975). By contrast, late-successional species can arrive early (Egler 1954) or late, have a lower maximum RGR, are more shade tolerant, but achieve greater maximum height and greater longevity than colonists (Bazzaz 1979, Chapin 1993).

In the early-seedling phase the impact of vegetation on seeds and germinants is almost always negative, reducing seed germination and survivorship, both directly through competitive preemption of resources and alteration of the physical environment for seed germination and establishment (Fig. 13; Drury and Nisbet 1973, Connell and Slatyer 1977) and indirectly by harboring herbivores, seed predators, and pathogens (Connell 1990). This pattern is generally observed in situations where vegetation is dense enough to produce a litter layer and exert a competitive influence (e.g., N-limited primary successions [this study, Walker and Chapin 1986, Vitousek et al. 1987, Morris and Wood 1989] and secondary succession [Drury and Nisbet 1973, Connell and Slatyer 1977]), but not in extremely dry environments like deserts and gravel pits, where early-successional vegetation facilitates initial seedling establishment (Shure and Ragsdale 1977, Finegan 1984, Davis et al. 1985, Walker and Chapin 1987).

After late-successional seedlings become established, early-successional vegetation can have both positive and negative effects (Fig. 13). At Glacier Bay and many other N-deficient primary successional sites (Gadgil 1971, Dancer et al. 1977, Bradshaw 1983, Richardson and Evans 1986, Morris and Wood 1989), the positive nutritional effects outweigh the negative effects of competition for light and soil resources. However, even this facilitative effect is complex, involving N fixation,

mycorrhizal associations, soil moisture, and soil pH. In less N-limited primary successional sequences (Walker and Chapin 1986) and in most secondary successional sequences (Drury and Nisbet 1973, Connell and Slatyer 1977), competitive inhibition may outweigh any facilitative effect of early-successional vegetation on established seedlings.

Finally, the replacement of early-successional colonists by late-successional species requires greater height and longevity but is probably mediated by a change to strong competitive inhibition of early-successional by late-successional species (Fig. 13). We are unaware of any long-term species removal experiments that directly test this assumption.

We conclude that, in general, life history traits and availability of propagules determine the pattern of succession, changes in competitive balance that accompany successional changes in environment provide the mechanism for changes in species dominance, and initial site conditions and facilitation (when present) influence the rate of change and final state of community composition and productivity.

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