FOREST CROWNS, SNOW INTERCEPTION AND MANAGEMENT OF BLACK-TAILED DEER WINTER HABITAT

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

Province of British Columbia

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FOREST CROWNS, SNOW INTERCEPTION AND MANAGEMENT OF BLACK-TAILED DEER WINTER HABITAT

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Abstract

The phenomenon of snow interception by forest stands is examined. Interception relationships extracted from literature are evaluated for their applicability to the silvicultural and climatic conditions of south coastal British Columbia. Hypotheses tested address: 1) the prediction of snow interception, 2) comparisons of heterogeneity in snow interception between second-growth and old-growth forests, and 3) how interception and interception efficiency vary depending on forest crown completeness and storm size.

General relationships regarding snow interception under continental conditions were found to hold in coastal conditions, but relationships between crown completeness and interception were weak. Storm size and melt are identified as confounding factors in making predictions about snow interception based on stand crown completeness. Several approaches to modelling snow interception are discussed. Particular reference is made to the effect of interception on energetic costs of locomotion for deer. Management of coastal forests for the interception of snow should focus on maximizing crown completeness and crown surface area. Further research is required concerning the relationships used in the simulation models. Emphasis should be placed on deer response to snowpacks, the influence of melt on snowpack development, and the influence of canopy closure on spatial distribution of snowpacks.

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1.0 INTRODUCTION

Forest canopies act as physical barriers to falling snow by intercepting it. Hydrology literature abounds with studies, particularly from northern latitudes and mountainous regions, that document the relationships between forests and particular characteristics of their associated snowpacks. The literature is summarized in comprehensive reviews by Kittredge (1953), Miller (1966), Meiman (1968), Anderson (1970), Shank and Bunnell (1982), and Bunnell _et al_. (1984).

The interest in forests' interception of snow derives from the necessity to manage snowpacks in regions where precipitation falls primarily in winter months and in the form of snow (e.g., Church 1912). Management of snowpacks is achieved indirectly through manipulation of environmental factors, such as forest canopies, that influence snowpack accumulation and ablation.

Reviewing the literature dealing with forest canopies and snow accumulation or ablation provides an appreciation for the variability in, and the varying magnitude of, the processes governing forest snowpack development. Figure 1 illustrates most processes involved in snow interception by individual tree crowns. The multitude of processes and the inherent confounding among their relationships to snow interception (in both temporal and geographical ways) leads to many inconsistencies in the literature (see review of Miller 1966, Bunnell _et al_. 1984).

Generally, it can be concluded that snow accumulation is

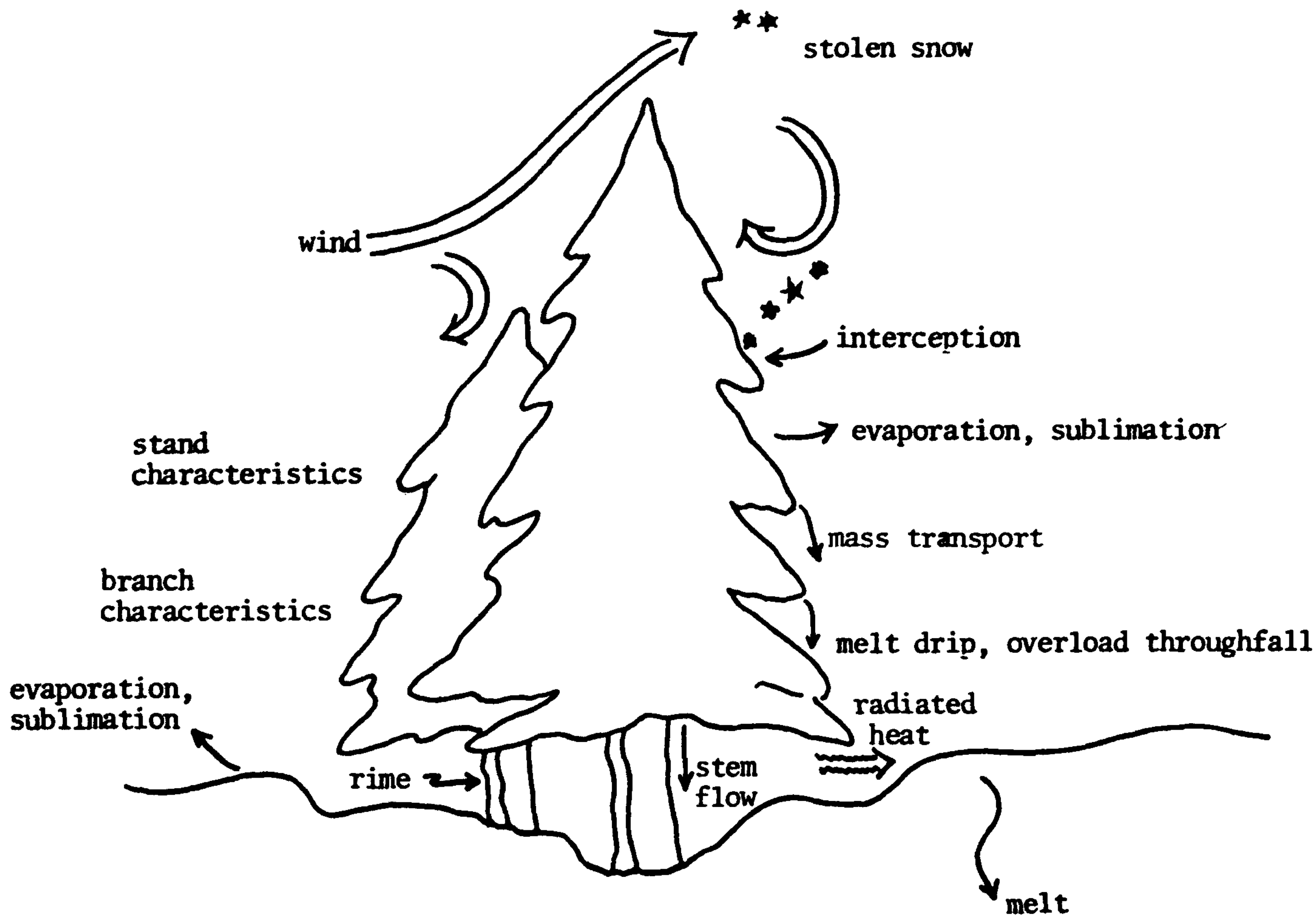


Figure 1. Schematic representation of relationships governing observed interception of snow by forests (from Bunnell et al. 1984: 10).

greatest in small forest openings (1.5-3.0 tree heights in width), followed by more open conditions, deciduous forest stands, and, finally, least snow accumulates in coniferous forests with tight or closed canopies (in der Gand 1978, Golding 1982). Bunnell et al. (1984) summarized generalities that are corollaries of the previous one. As crown completeness (see Section 2.1) increases, snow interception increases and, likewise, as snow storm size (magnitude of snowfall) increases, total interception of snow increases. The efficiency of interception, or percent of snowfall intercepted, decreases with increasing storm size. It is this interception of snow by forest canopies that allows managers some degree of control over where, what type, and how much snow accumulates.

Snowpack management objectives most frequently concern avalanche control, flood control, or the timing and quality of water reserves (Goodell 1959, Haupt 1972, Golding and Swanson 1978, Strobel 1978, Harr and Berris 1983). The particular perspective adopted in this thesis is one associated with wildlife ecology in the northern temperate regions of North America. Formozov (1946), Severinghaus (1947), Nasimovich (1955), and Jones and Bunnell (1984) provide discussions concerning the effect of snow accumulations on wildlife populations.

1.1 Rationale

Snow can be a major detriment to deer in regions where snowpacks accumulate to more than 25 cm annually. Columbian black-tailed deer (*Odocoileus hemionus columbianus*) living in mountainous areas of coastal British Columbia (B.C.) require special winter range habitats to survive winters with deep long-lasting snowpacks and to ensure successful reproduction the next spring (Jones 1975, Bunnell *et al*. 1978, Bunnell 1979, Bunnell and Jones 1984). Historical weather patterns indicate that winters with deep snow are frequent enough to consider winter range needs to be the major concern in deer habitat management over much of southern coastal B.C. More comprehensive discussions on this specific subject are provided by Bunnell *et al*. (1978), Harestad *et al*. (1982), Bunnell (1984), McNay and Davies (1985), and Nyberg *et al*. (1984).

Generally, it is documented that snowpacks of 44 to 50+ cm will impede deer locomotion, while lesser accumulations increase the energetic cost of locomotion (Gilbert *et al*. 1970, Ozoga 1972, Jones 1975, Cederlund 1982, Parker 1983, Telfer and Kelsall 1984). In addition to the increased energy cost associated with negotiating snowpacks there is a reduction in the potential intake of energy resulting from both movement restrictions which limit browsing area and the inaccessibility of forage buried by deep snow (Hanley 1981, Bunnell 1984). Jones and Mason (1983) attributed black-tailed deer population declines on northern Vancouver Island in 1969 and 1972 to the severe winters during 1968-69 and 1971-72 (Fig. 2). Subsequent declines in deer numbers are confounded by increasing predation by wolves (Jones and Mason 1983). Jones (1975) studied in the same location during the 1971-72 severe winter and reported that where 200 cm of snow accumulated in open areas, only 30 cm accumulated in the adjacent forests with 70% crown completeness.

The fact that deer depend on forests for winter shelter is commonly acknowledged by deer managers in northern temperate latitudes (Severinghaus 1947, Edwards 1956, Cederlund 1982). In the coastal forests of British Columbia three phenomena have created an unusually difficult management scenario:

1) The forests that deer select as winter shelter are "old-growth" (or old-aged) stands predominantly composed of Douglas-fir (*Pseudotsuga menziesii*) growing on southern slopes between 300 to 650 meters in elevation (Nyberg 1983, Nyberg *et al*. 1984, McNay and Davies 1985). Deer biologists recognize this "old-growth" as deer habitat because it has the combination of an abundant understory vegetation, an abundant arboreal lichen supply (both being deer winter forage items), and an overstory crown completeness capable of intercepting snow (see Bunnell 1984). Foresters recognize this "old-growth" as a high volume and a highly valued renewable resource base that is situated within topographic conditions affording easy

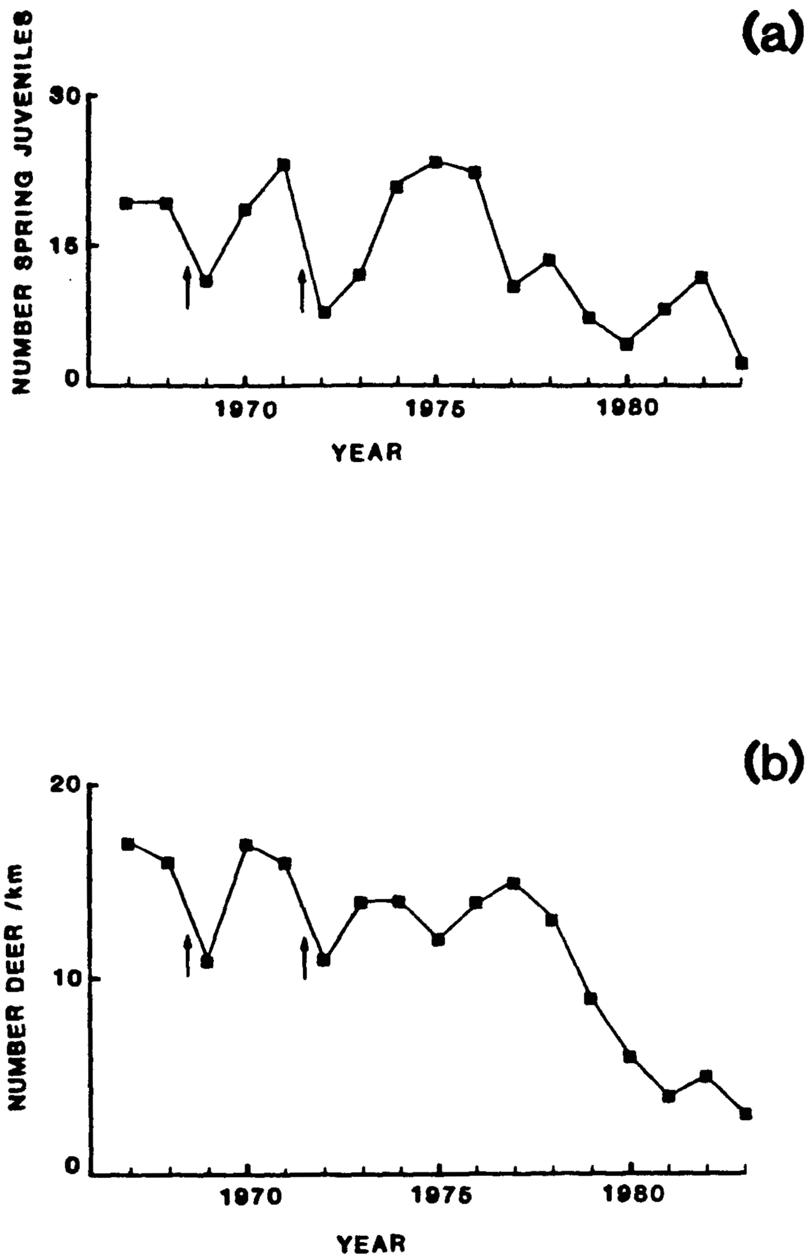


Figure 2. An example of the deer decline on northern Vancouver Island (Davie River subunit) during the severe winters (arrows) of 1968-69 and 1971-72 (after Jones and Mason 1983: 7-8).

access. Thus, since 1970, the issue of deer winter range has developed into the most important wildlife-forestry conflict in south coastal B.C. (Nyberg et al. 1984, McNay and Davies 1985).

2) While the generalities extracted from snow literature are assumed to prevail in the forests of coastal British Columbia, few studies have tried to document this assumption (Golding 1968, Woo 1972, Fitzharris 1975). Meager (1938), Rothacher (1965), Fitzharris (1975), and Golding (pers. commun.) agree that the processes governing snow delivery, accumulation, and ablation are the same but that their interrelations are quite different in the warm maritime climate of coastal British Columbia as compared to the colder, drier continental conditions where the majority of research on snow occurs.

3) Snowpack characteristics influencing deer locomotion are: a) depth (deer cannot negotiate soft snowpacks much deeper than their own chest height), b) density (dense snow increases drag and therefore increases the cost of locomotion but high densities may afford deer support and therefore reduce sinking depth), c) hardness (a hard crusted snow enables deer to walk on top of snowpacks with no increase over the usual cost of locomotion), d) spatial distribution, and e) temporal duration. Usually only depth

(in units of snow water equivalent) and density are discussed in literature on forest-snow relationships thereby providing deer biologists with little information concerning the capability of forests to alter snowpacks beneficially for deer.

1.2 Objectives and Hypotheses

The first broad objective is to evaluate the applicability of generalities concerning snow interception to coastal forest silvicultural and climatic conditions.

The specific hypotheses that are tested include:

1) Measurement of mean crown completeness (MCC) for the purposes of predicting snow interception can be accomplished by a technique based on an instrument called the moosehorn (for a description and discussion on the moosehorn see Bonnor 1967).

2) Intra-stand variability in crown completeness (CC) is greatest in old-growth forests and this will be reflected in the variation of accumulated snow depth (apparent interception) as well as in new or storm-specific snow depth (interception).

3) Interception of snow by a forest stand is a predictable

phenomenon:

(a) on an individual storm basis the moosehorn measure of MCC will prove to be a useful index for predicting the mean stand interception. Stands with tightest crown completeness will intercept most snow.

(b) apparent interception of a particular forest stand can be predicted based on MCC and a measure of snow water equivalent at the time of maximum snowpack accumulation.

The second broad objective is to integrate various snow interception models with a deer locomotion model (see Parker *et al*. 1984). The purpose of the modelling exercise is 1) to investigate relationships between forest canopy and deer energetic output under different annual snowfall regimes, and 2) to propose one model that is best suited for management concerns on Vancouver Island.

2.0 MATERIALS AND METHODS

This thesis is largely a review and synthesis of published data. Data on forest-snow relationships are usually presented in a manner that is inappropriate from the perspective of a wildlife biologist (Section 1.1 and 2.2) and for this reason three studies were designed to help achieve the objectives noted in Section 1.2. The following sections: 1) describe the extraction and interpretation of data from literature, and 2) describe briefly the three studies used to supplement the review and synthesis of published data.

2.1 Interpretation of Snow Literature

Care must be taken in extracting generalities from the literature for three reasons: 1) the diverse nature of forest stands, 2) the temporal and regional heterogeneity in the data bases, and 3) a diverse and often confusing terminology used in the reporting of results.

Bunnell et al. (1984) documented that a large number of interacting factors influence interception by single trees. In forest stands the phenomena of interception are more complex because individual crowns are not identical and are not uniformly distributed. Individual crown attributes interact together and with abiotic factors in a complex manner. Also, a stand measurement necessarily takes longer to acquire than do those from individual trees (Bunnell et al. 1984). Reported measurements from stands are integrated over a long sampling time period and over a large, and heterogeneous area. As a result, the relative contributions of individual variables or processes cannot be separated clearly.

Problems with terminology in snow literature centre around two concepts (Bunnell et al. 1984): 1) crown measurements, and 2) definitions of snow interception. The following discussion summarizes that of Bunnell *et al.* (1984).

Crown Measurements.--Foresters routinely measure and evaluate crown characteristics yet there is no standardized terminology or widely accepted methodology for crown measurement. Crown measurements vary widely depending on the worker's definitions and methods. Canopy cover often refers solely to the proportion of the ground overlain by tree canopy. However, some workers also incorporate the degree to which an individual tree's crown is 'complete'. Furthermore, it is well documented that values of canopy cover measurements are highly dependent upon the means of measurement employed (see Section 4.1.1). Discrepancies between canopy covers determined by various means have been reported by Dodd *et al.* (1972), Rochelle (1975), and Majawa (1977).

The terminology and definitions used in this report follow those presented by Bunnell *et al.* (1984):

1) 'Crown Closure' = 'Canopy Cover' - the proportion of the ground surface encompassed by vertical projections of the outer edges of tree crowns. This measurement is better suited to stands and is usually used in that context.

2) 'Crown Completeness' - the proportion of the sky obliterated by tree crowns within a defined angle (or determined with a described instrument) from a single point. This is a point measurement obtained with such

instruments as a moosehorn, spherical densiometer, or camera. It combines reduction in cover resulting from both the absence of tree crowns and from holes within tree crowns.

3) 'Mean Crown Completeness' - a stand measure determined from a number of crown completeness measures.

Snowpack And Snow Deposition.--In the literature the term "interception" is often used uncritically. It is correctly used only when it refers to that amount of snow or proportion of a snowfall that does not reach the ground during a given single storm (Gray and Male 1981). It can be approximated by the difference: new snow in the open minus new snow under the canopy (henceforth referred to as interception). Too often interception is used to refer to the difference between snowpack in the open and snowpack under the canopy (henceforth referred to as apparent interception). Differences in snowpack arise from a host of factors including true interception, the fate of intercepted snow, melt rates, and redistribution of snow by wind.

Tree canopies have a physical limit to the amount of snow that can accumulate on or in them. This maximum is termed 'maximal snow load' and is measured in kg or kg of snow water equivalent per unit area. Once the maximum is attained, further snowfall drops from the crown and is operationally defined as 'overload throughfall' if it occurs during the storm and 'mass transport of intercepted snow' if it occurs after the storm.

2.2 Sampling Methods

Three studies were designed to record snow depths and crown completeness in two broad strata of forest canopies: young forest canopies (20-30 years old) and old forest canopies (120 or more years old). The sampling design in the two studies at the University of British Columbia Research Forest (UBC Research Forest) was a nested design with secondary level plots sampled systematically along permenant transects. The design at the Mt. Seymour study site was nested as well but secondary plots were established randomly and tertiary plots were established systematically along temporary transects. Sample sizes were determined from a pilot study performed during the winter of 1981-82 utilizing a sampling design similar to those mentioned above.

Data on snow interception were collected directly following two snow storm events during January 1982 at the UBC Research Forest. Eight different experimental forest spacing designs [3 x 3 m (50% and 0% thinned), 6 x 6 m, 9 x 9 m, 12 x 12 m, 15 x 15 m, nelder-east, nelder-west, and nelder-south] were utilized in an attempt to achieve a range of canopy closures and crown characteristics. A nelder plot is a planting configuration in concentric circles such that trees on the outer circumference are more widely spaced than those near the centre. All eight stands sampled were 18- to 20-year-old Douglas-fir at approximately 200 m in elevation and on level terrain. Within most stands, four permanent plots were established (two plots in the 12 x 12 m and 15 x 15 m thinned stands and seven in each of the nelder stands). At each plot, eight snow depth measurements were taken as well as one measurement of each of the following: moosehorn, convex spherical densiometer, light meter, crown height, crown width, number of trees per hectare, ocular estimation of canopy completeness, and photographs of canopy completeness (utilizing incident degrees of 10, 20, and 30 around the zenith). New snow depths in the forested sampled plots were compared with new snow accumulations in an adjacent clearcut. All forest data were tested for normality and correlated with interception efficiency obtained on each plot. Significant correlations were selected for linear regression analysis and residuals plotted as a "goodness of fit" test (Midas: Fox and Guire 1976). Analysis of variance tests were used to compare plot and/or stand mean snow interception and interception efficiency (ANOVA, Midas: Fox and Guire 1976, ANOVAR, University of British Columbia: Coshow 1971).

A second study at the University of British Columbia Research Forest (Fig. 3) during March 12 to April 5, 1982 utilized four different stands of two broad age classes. The intent was to sample two second-growth stands and two old-growth stands within similar elevations and aspects and compare snow

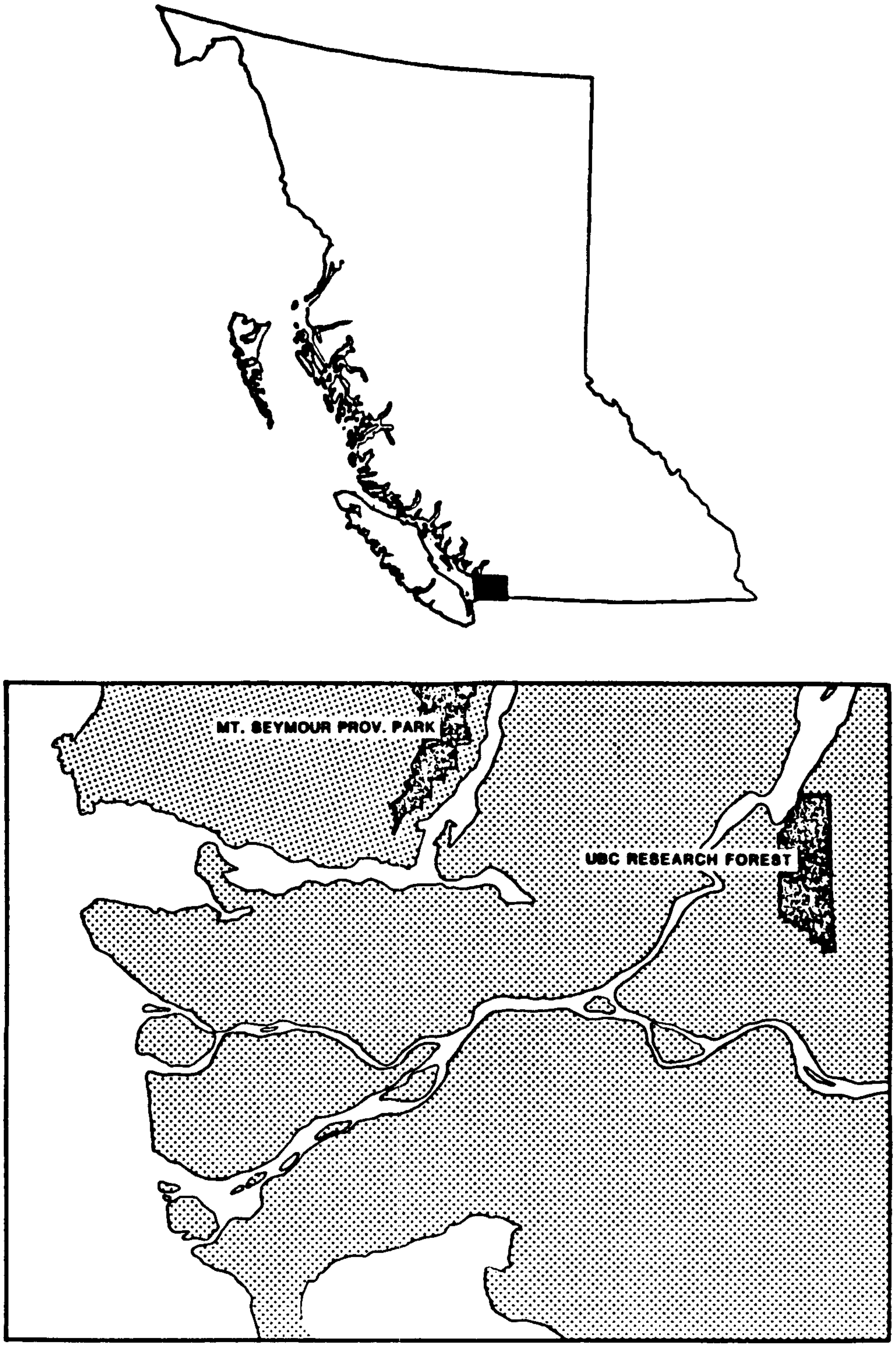


Figure 3. Study area locations.

accumulations between the stands and adjacent openings. To ensure that stand comparisons are legitimate, snow accumulation in the adjacent openings should not be significantly different. The data were analyzed by the analysis of variance technique (ANOVAR, Midas: Fox and Guire 1976). No significant difference ($P > 0.05$) was noted in mean snow depths or variance between the adjacent openings. Sampling was done at the time of maximum pack accumulation so as to conform with the analysis of Harestad and Bunnell (1981). Data from this study are snowpack depth measurements and analyses are for 'apparent interception efficiency'. The sampling design employed was systematic sampling along three transects in each stand. Each transect had 13 sampling stations. At each station the following observations were recorded: four snow depth measurements, one canopy completeness measurement (by the moosehorn technique), number of trees per hectare, and dbh. Six snow density measurements (Stevenson snow sampler) were taken along each transect as well as estimates of average dominant tree height and crown length. Analyses followed the procedure developed in the first UBC Research Forest study.

A third study, located on Mt. Seymour (elevation 970 m; Fig. 3) during January and February 1984, compared total snow accumulation, as well as new snow accumulation after two storms, in an 80-year-old, second-growth stand, an old-growth stand, and open conditions. Four sampling days were spent in each of the three forest conditions. Random sampling was used to measure snow depth (n = 10), snow density (n = 5), and canopy completeness (n = 5) at each plot. Number of plots was 6 for the old-growth and for the second-growth, and 3 for the open condition. The analysis procedure followed the design previously reported.

Further information on all forest plot conditions is provided in Tables 2 and 3 of Section 4.1.1.

3.0 FACTORS OTHER THAN FOREST STRUCTURE THAT INFLUENCE INTERCEPTION

The investigation of forest canopies (and in particular crown completeness) and their influence on snow interception is the primary objective of this thesis (Section 1.2). Two factors have the potential to mask the influence of forest canopies; they are storm size and elevation. The influence of storm size and elevation is discussed so that analyses and conclusions concerning forest canopies and snow interception can be presented in a clear fashion.

3.1 Storm Size

Figures 4 and 5 demonstrate the relationship between interception versus magnitude of snowfall. As expected there is significantly more scatter than in similar graphs plotted repeatedly for the same tree (e.g., Fig. 6). Note as well the

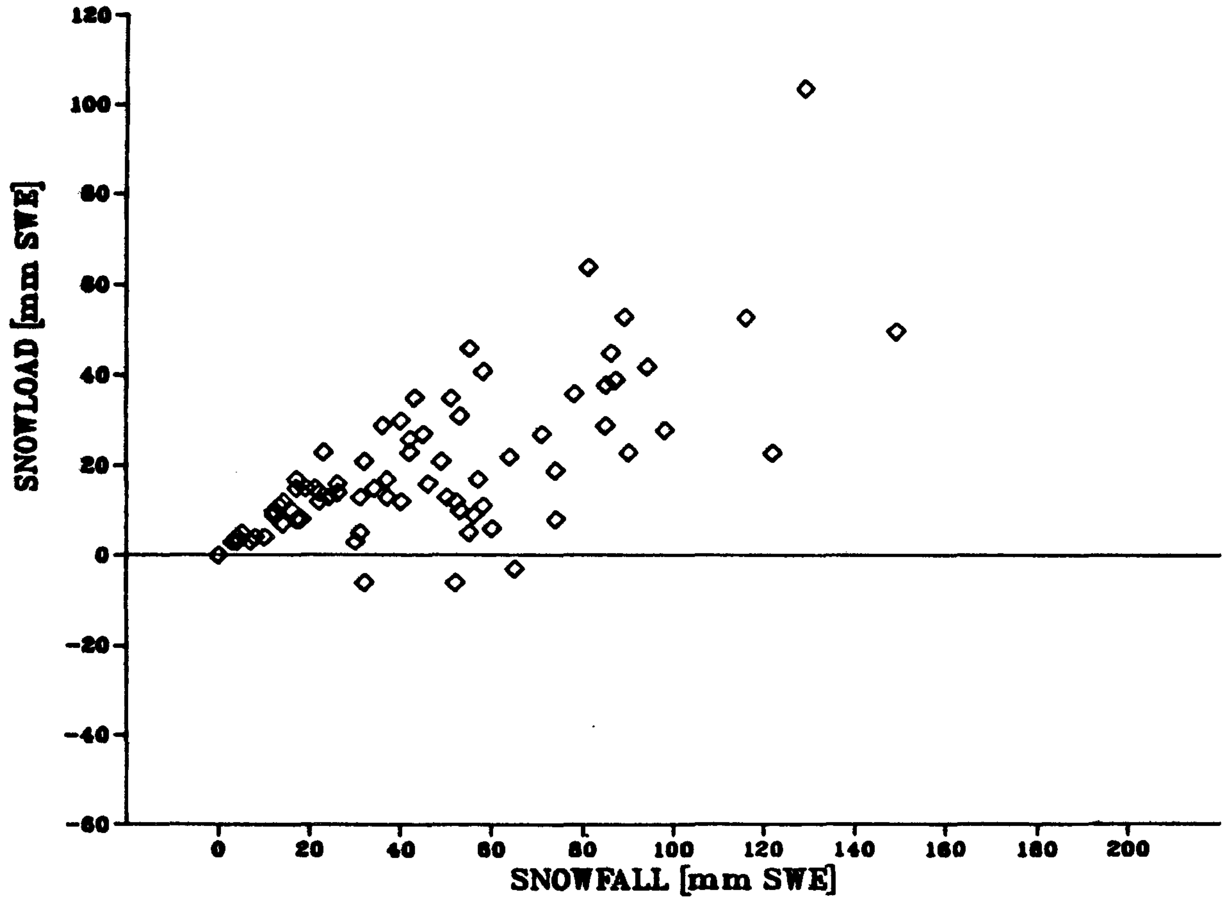


Figure 4. Snow load on trees during individual storms at 1060 m on Mt.Seymour (data of Fitzharris 1975: Appendix G, from Bunnell et al. 1984: 336).

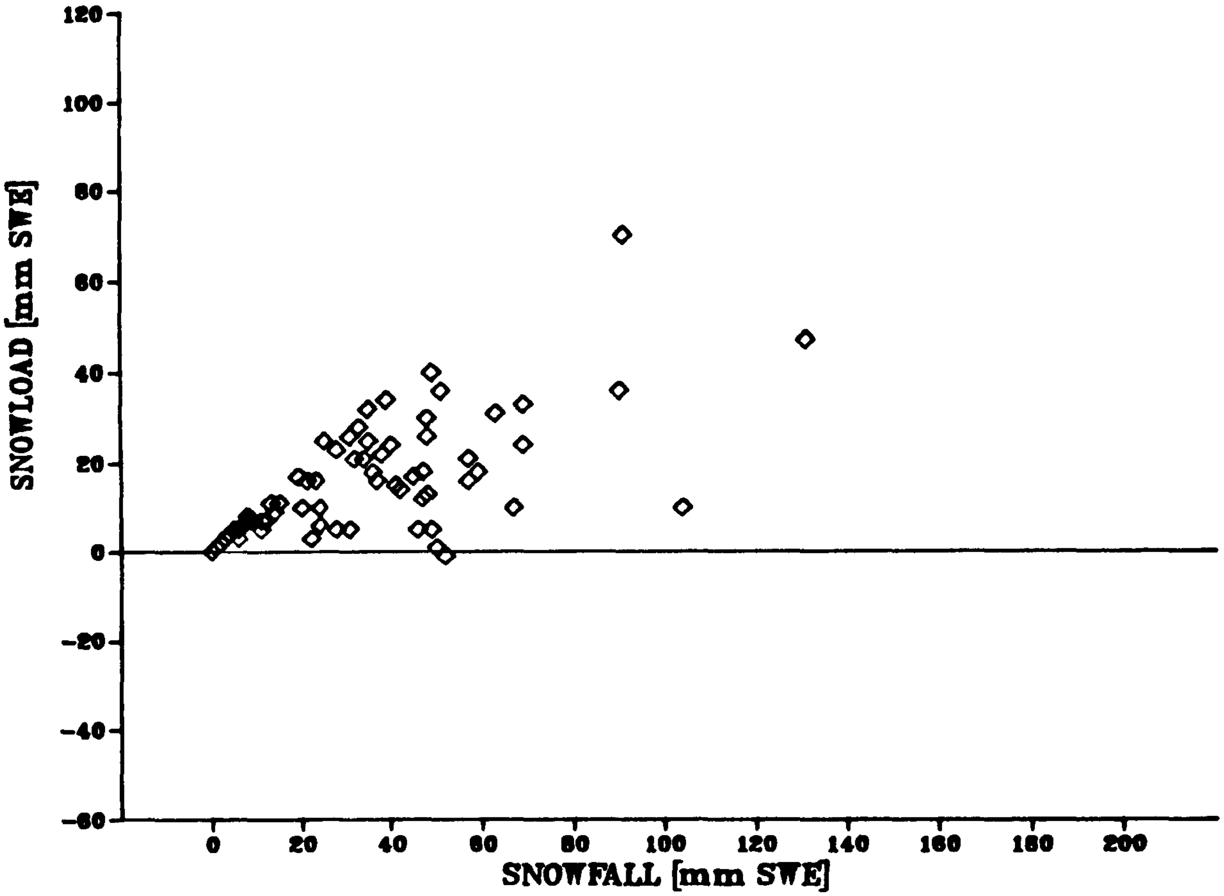


Figure 5. Snow load on trees during individual storms at 970 m on Mt. Seymour (data of Fitzharris 1975: Appendix G, from Bunnell et al. 1984: 337).

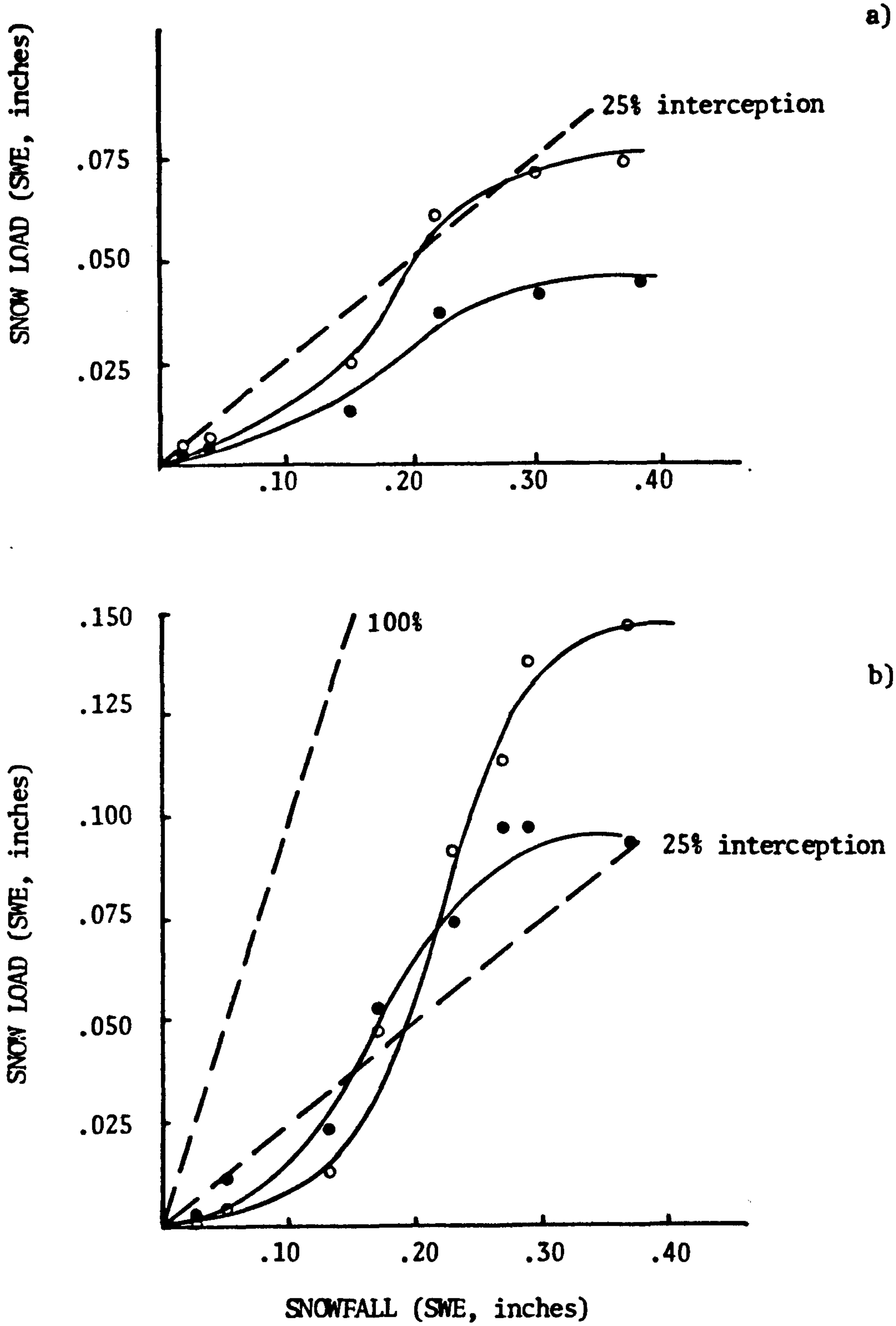


Figure 6. Snow catch by Douglas-fir (o) and white pine (•) trees during two storms on January 10,1967 (a) and January 12, 1967 (b) (data of Satterlund and Haupt 1967: 1038, from Bunnell et al. 1984: 239).

lack of a clear upper asymptote for snow interception in stands. Four potential reasons why the data for individual stands reveal no clear upper asymptote to snow interception are discussed in 4.1.2 (compare Figs. 5 and 6).

Fitzharris (1975) developed a regression equation describing the amount of snow under the canopy in terms of snowfall and elevation (Eq. 1).

$$S(c) = -1.3 + 0.2\ S(o) + 0.0002\ S(o)H + 0.0013\ S(o)^2 \quad (1)$$

$$(n = 511,\ r^2 = 0.78\ SE = 9.8)$$

Snow under a forest canopy [S(c)] is significantly related to snowfall (mm SWE) in the open [S(o)] and elevation (H). Analysis of Fitzharris' data was repeated omitting data from elevations below 590 m where little snow persisted through the winter and omitting the elevation term. Equation 2 resulted, exhibiting no change in the coefficient of determination and little change in the standard error.

$$S\ (c) = -4.5859 + 0.647\ S(o) \qquad (2)$$

$$(n = 380,\ r^2 = 0.78,\ SE = 9.9,\ P < 0.0001)$$

The re-analysis indicated that the elevation effect was primarily through its contribution to S(o) and therefore S(o) alone strongly influences interception.

Data of Fitzharris (1975) illustrating the effects of storm size on interception efficiency (Fig. 7) contain more variability. His data were analyzed by broad elevation class. Crown completeness differed between elevations; the "canopy closure index", CCI, was 0.64 at 970 m (Eq. 3) and 0.29 at 1060 m (Eq. 4). Character of the snowfall also differed between elevations. Significant but weak relationships were found between interception efficiency and the magnitude of a snowfall event.

Interception efficiency (IE) at 970 m and CCI = 0.64

$$IE = 79.9 - 0.46\ S(o) \qquad (3)$$

$(n = 78,\ r^2 = 0.25,\ SE = 26.9,\ P < 0.0001)$

Interception efficiency (IE) at 1060 m and CCI = 0.29

$$IE = 78.07 - 0.63\ S(o) \qquad (4)$$

$(n = 73,\ r^2 = 0.25,\ SE = 28.5,\ P < 0.0001)$

Despite violating the homogeneity of variance assumption for regression analysis, there still is a clear influence of storm size on the amount of snow intercepted by the canopy (increasing with storm size, Figs. 4 and 5, Eq. 2) and the interception efficiency (decreasing with increasing storm size, Fig. 7, Eqs. 3 and 4).

The broad pattern is more clearly exemplified by data of

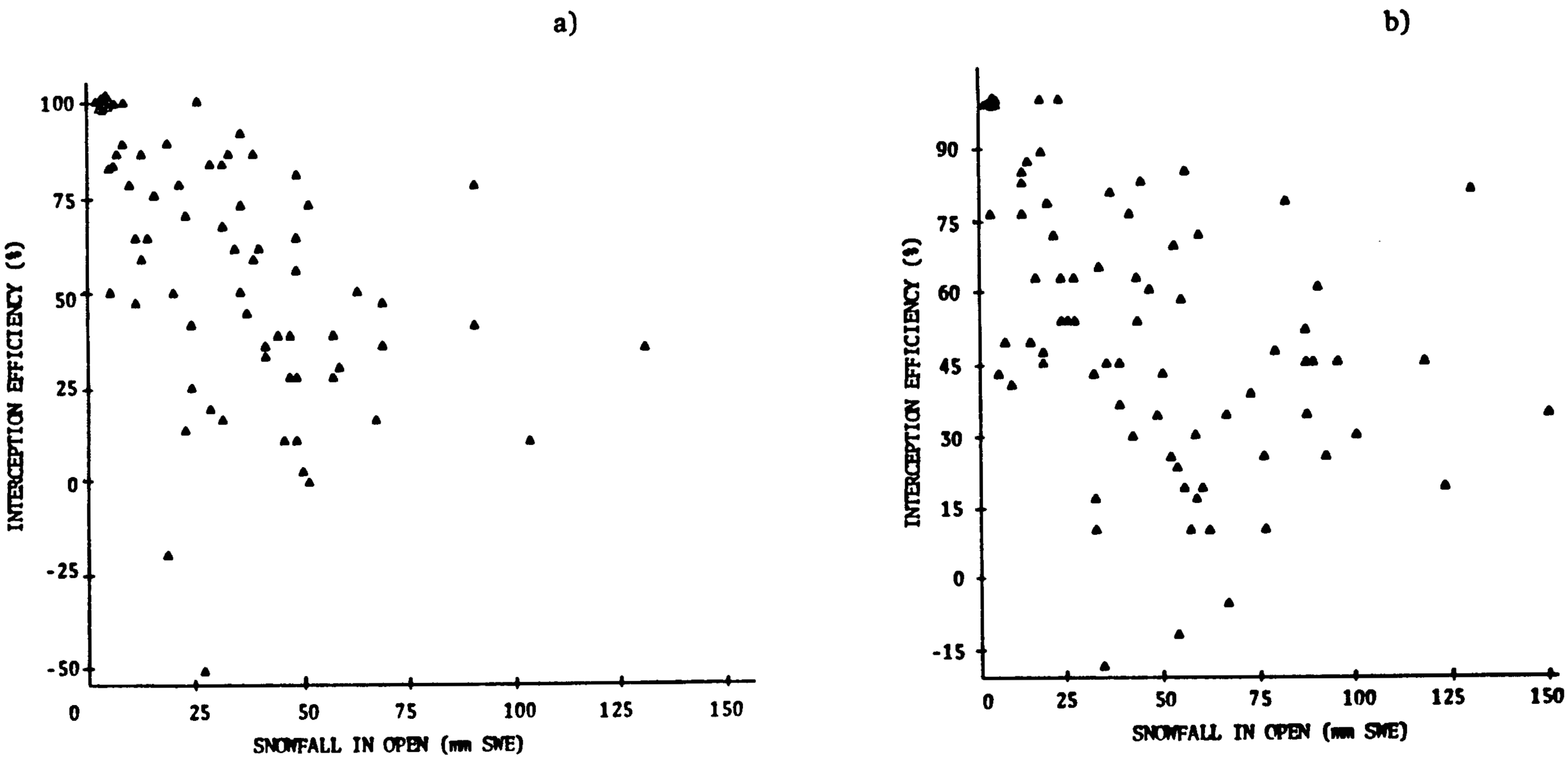


Figure 7. Effect of storm size on interception efficiency at 970 m (a), and 1060 m (b) elevation (reanalysis of Fitzharris 1975: Appendix G, from Bunnell et al. 1984: 353).

Strobel (1978). He documented the relationship between snow interception and storm size for two different forest stands (Fig. 8). The use of mean stand values clarify the trends shown by Fitzharris' data. Note also that the data of Strobel indicate an upper asymptote to snow interception similar to the data for individual trees (Fig. 6 and 8).

3.2 Elevation

Recognizing the potentially important effects of snow temperature on interception efficiency and maximal snow load, Fitzharris (1975) analyzed his data with respect to three functional elevation zones: 1) the "drift snow zone" at 1260 m where snowfall was colder and drier, and redistribution by wind could render open versus canopy comparisons of negligible value in evaluating interception, 2) the "wet snow zone" located below the equivalent temperature where much precipitation fell as rain, and 3) the "snow zone" located above the equivalent temperature but below 1260 m (Fig. 9).

The results were:

Drift snow zone

$$S(c) = 6.0 + 0.2\ S(o) + 0.0041\ S(o)^2 \qquad (5)$$

$$(n = 82,\ r^2 = 0.73,\ SE = 15.2)$$

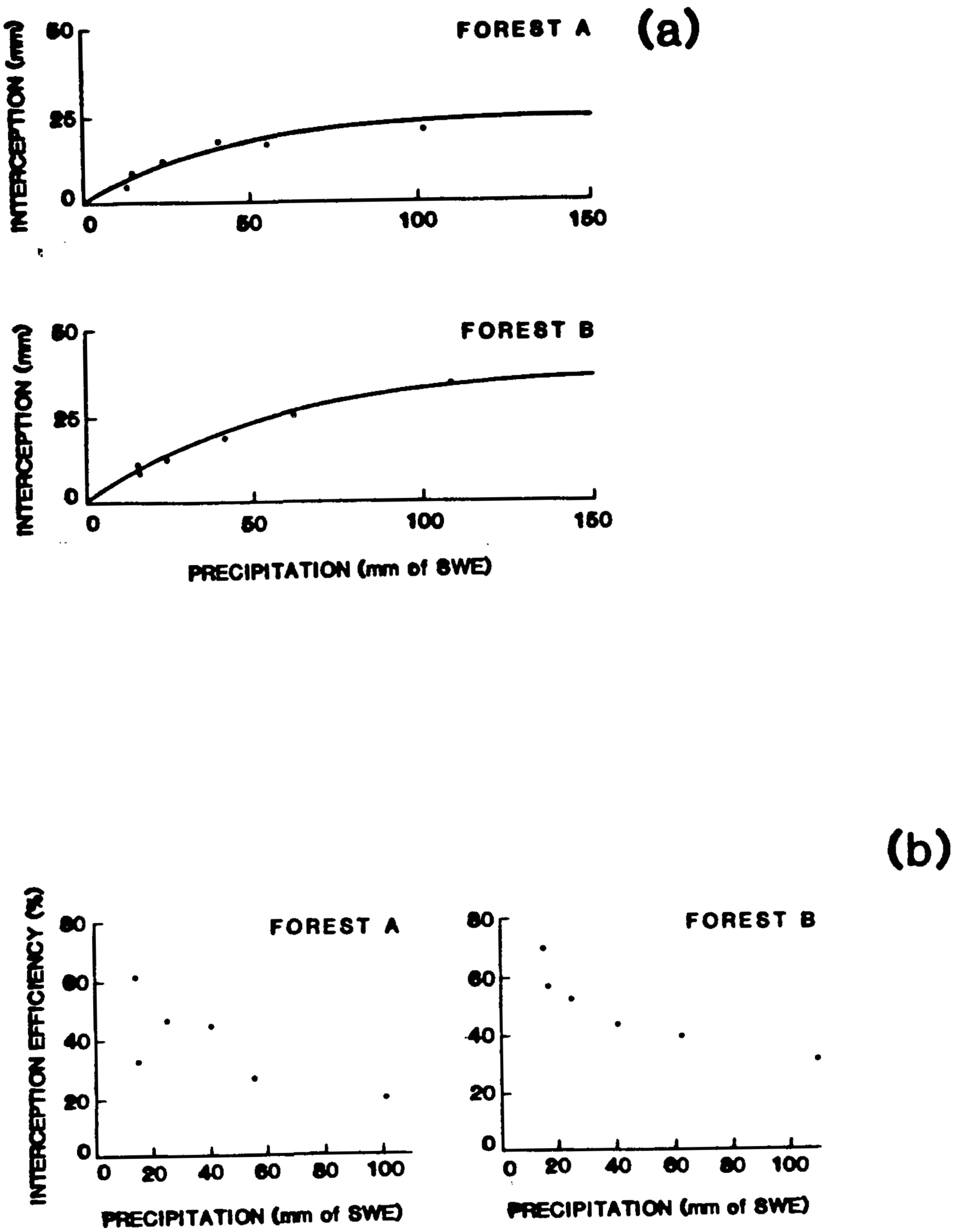


Figure 8. The effect of increasing storm size on (a) interception of snow and (b) interception efficiency in two seperate forests (adapted from Strobel 1978: 78).

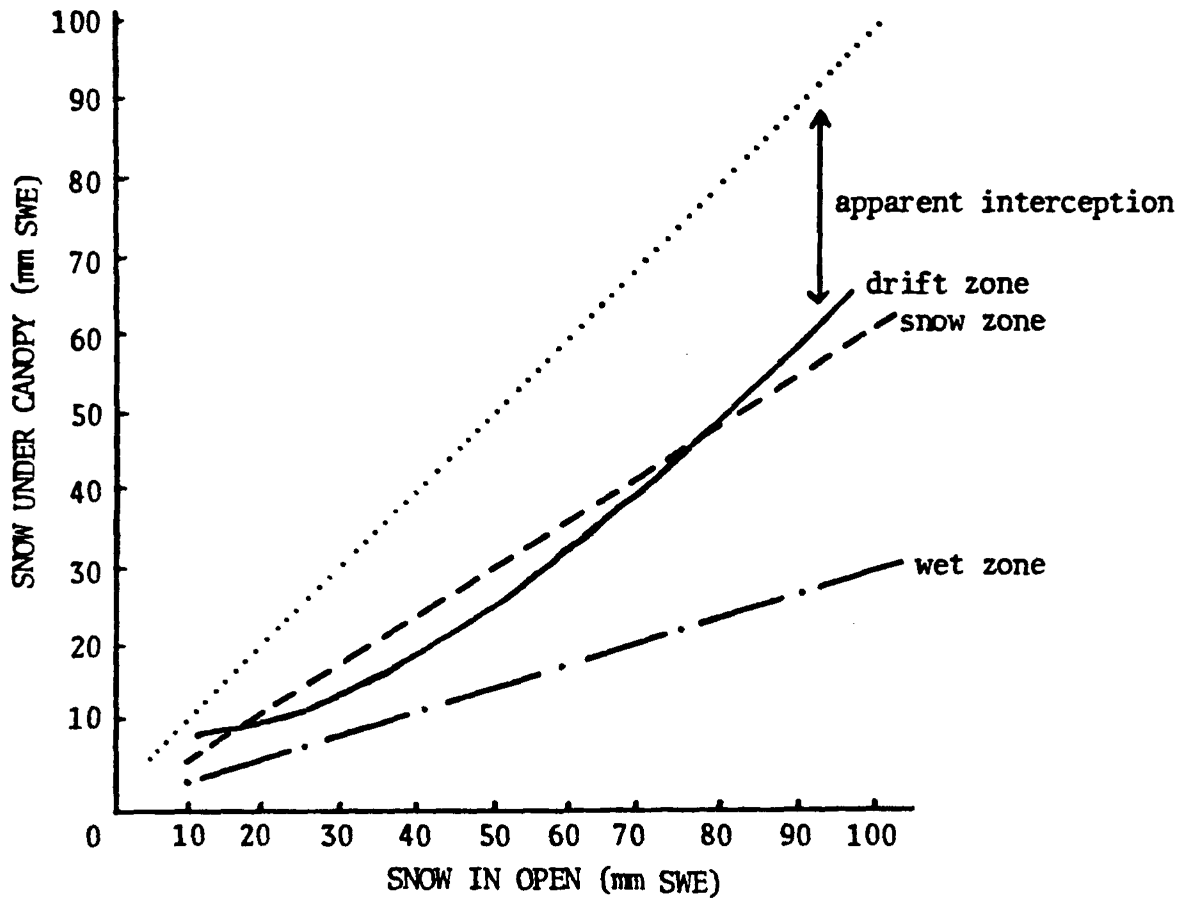


Figure 9. Regressions of snow under the canopy as a function of snow in the open for 82 storms on Mt. Seymour (data of Fitzharris 1975: 271,from Bunnell <u>et al</u>. 1984: 348).

Snow zone

$$S(c) = -1.4 + 0.0006\ S(o)\ H \quad (6)$$

$(n = 188,\ r^2 = 0.74,\ SE = 9.1)$

Wet snow zone

$$S(c) = -7.4 + 0.0004\ S(o)\ H \quad (7)$$

$(n = 178,\ r^2 = 0.54,\ SE = 5.2)$

3.3 Conclusions

Magnitude of snowfalls and differences in elevation are potentially confounding factors in analyses of snow interception by forest stands. The variation contributed by these factors is expected to be considerable given the significance of Eqs. 3-7. Subsequent analyses, for this thesis, stratify canopy - interception relationships by elevation zones as well as snowfall sizes in an attempt to reduce the confounding of these variables. It is expected that the influence of these factors may have implications on management recommendations.

4.0 RESULTS AND DISCUSSION

4.1 The Interception of Snow by Forest Stands

To reduce ambiguity and potential confounding of factors (see Section 1.1), the following analyses are grouped into sections depending on whether or not: 1) the data are from individual storms or from total snowpack measurements, and 2) the data are in the form of snow depth measures or measures of snow water equivalent (SWE). Throughout the analyses of interception data, attempts are made continually to separate the influences of elevation and snow storm size (Section 3) from the influence of crown completeness.

4.1.1 Crown Completeness and Snow Interception: Snow Depth

Single Storms.--Figure 10 presents graphs of the relationship between crown completeness and percentage interception in two separate storms at the UBC Research Forest when crown completeness was measured by various means. Five of the seven measurement techniques employed were significant predictors of snow interception efficiency ($P \leq 0.01$) and are presented here. Neither the spherical densiometer nor the light meter seemed promising as predictors of interception efficiency. The data from Figure 10 are expressed as equations in Table 1. Data are aggregated for the 8 different spacing designs [3 x 3 m (50% and 0% thinned), 6 x 6 m, 9 x 9 m, 12 x 12 m, 15 x 15 m, and three nelder plots] giving a total of 41 points for each regression.

Comparison of the statistics in Table 1 shows that the moosehorn has the highest r^2 value and lowest standard error. The moosehorn is followed in degree of predictive power by the

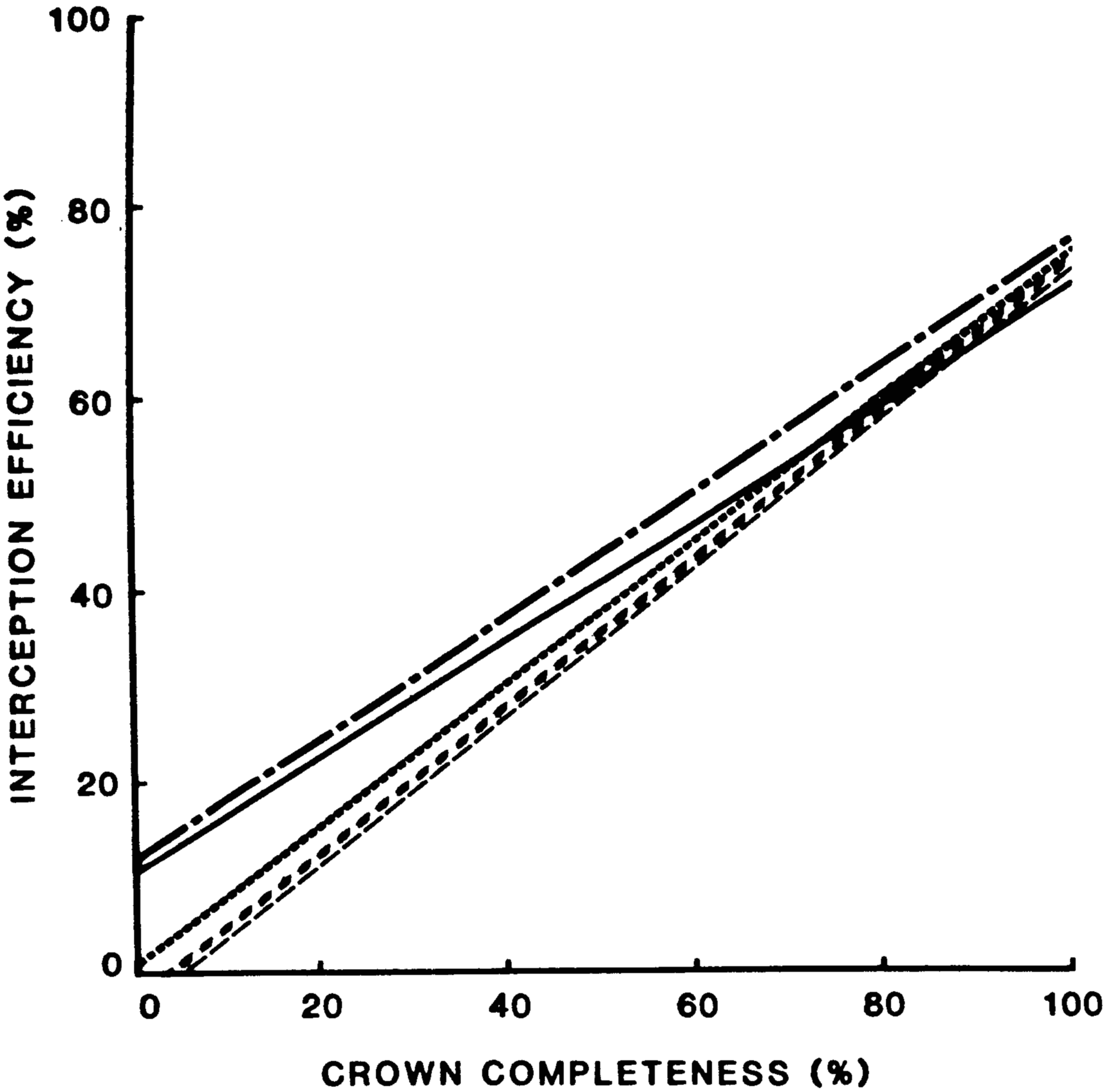


Figure 10. The effect of crown completeness measurement technique (— · —) ocular estimate, (———) photo 10°, (••••••••) photo 20°, (- - - -) photo 30°, and (— — —) moosehorn on regressions of interception and crown completeness.

Table 1. Regression equations relating percent interception (IE), during two single storms, to crown completeness (CC)[1] as a function of canopy measurement technique.

Canopy measurement technique	Equation	r^2	$S_{y.x}$	P(slope ≠ 0)
Moosehorn	IE = 0.77(CC) - 4.39	0.74	8.88	<0.01
Occular estimate	IE = 0.65(CC) + 12.2	0.63	10.61	<0.01
Photo (10° cone)	IE = 0.62(CC) + 11.1	0.55	11.74	<0.01
(20° cone)	IE = 0.73(CC) + 1.52	0.53	12.02	<0.01
(30° cone)	IE = 0.78(CC) - 4.21	0.48	12.62	<0.01
Spherical densiometer		0.22		>0.01
Light meter		0.16		>0.01

1/Measurements were taken over a range of canopy conditions in 8 different experimental plots.

ocular estimate technique, the photographic technique utilizing a subtended angle of 10°, and finally by the photographic techniques utilizing larger angles.

Wider angles used in canopy measurement incorporate more of the vegetation cover. At any point, measurements using larger angles tend to yield higher crown completeness in young stands (Fig. 11). As would be expected, lower y-intercepts and higher slopes necessarily result. This fact is evident in Table 1 particularly when the statistics for the photographic techniques are compared. The angle subtended by the moosehorn is only slightly less than 10° and is the technique closest to a point measurement that was tested. It is unclear why it should provide the best estimator of interception efficiency. Ocular estimates were taken immediately after the moosehorn and may be biased. Except for the apparent anomaly of the moosehorn (which theoretically should yield the same values as 10° photos), there is a general tendency for the predictability of interception efficiency to increase with decreasing angle of measurement. The trend is expected in young canopies experiencing wet snow (there is little crown depth and the snowfall approximates vertical).

It is expected that the moosehorn measure of MCC will have some inconsistency associated with it. As the height to the base of live crown (HBLC) increases the estimate of crown completeness from point measurements will have lower variation (pers. commun. C.C. Shank and D.J. Vales; Fig. 12). Variance

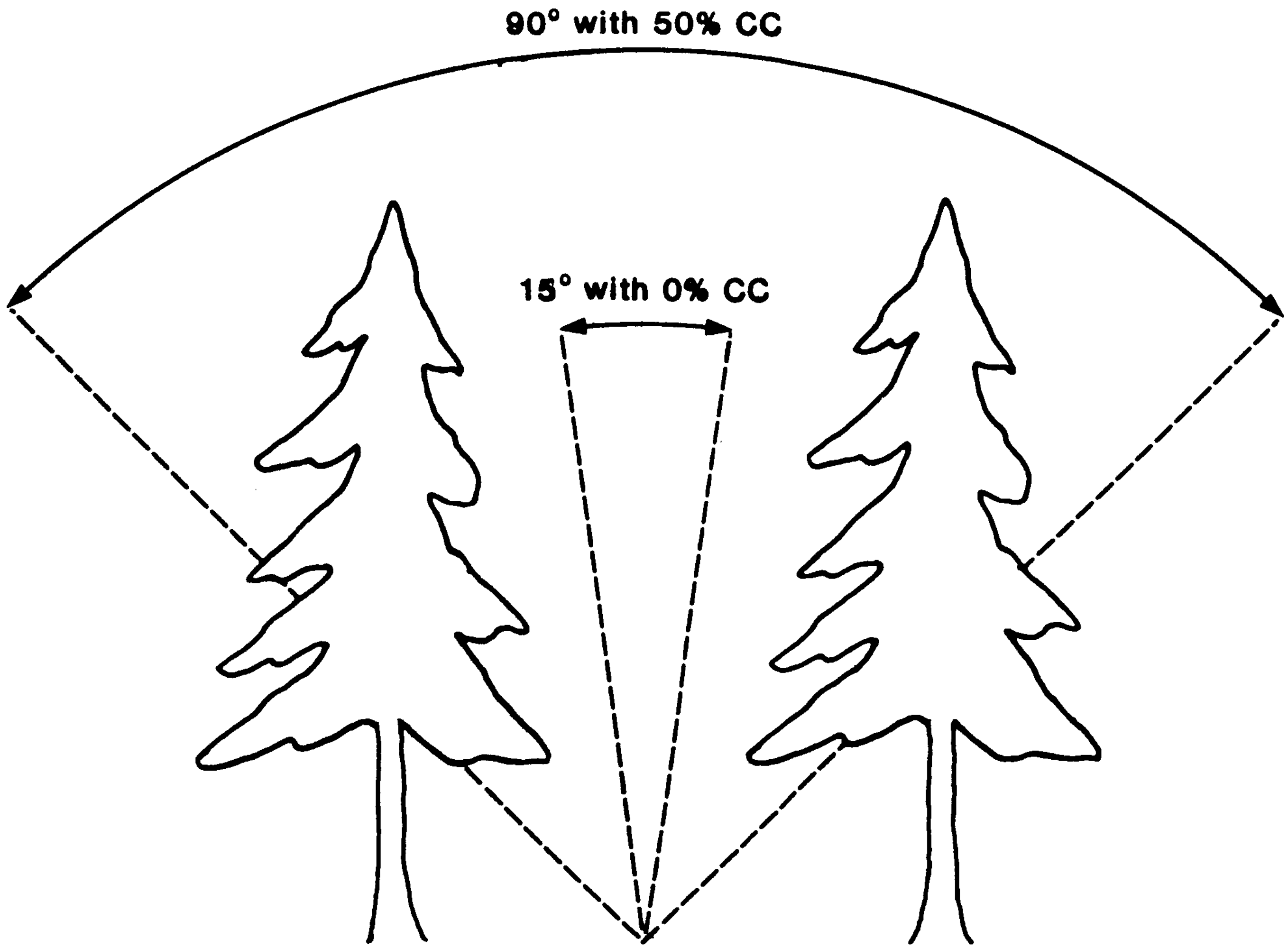


Figure 11. Schematic presentation of the relation between angle of crown completeness measurement device and point estimates of crown completeness.

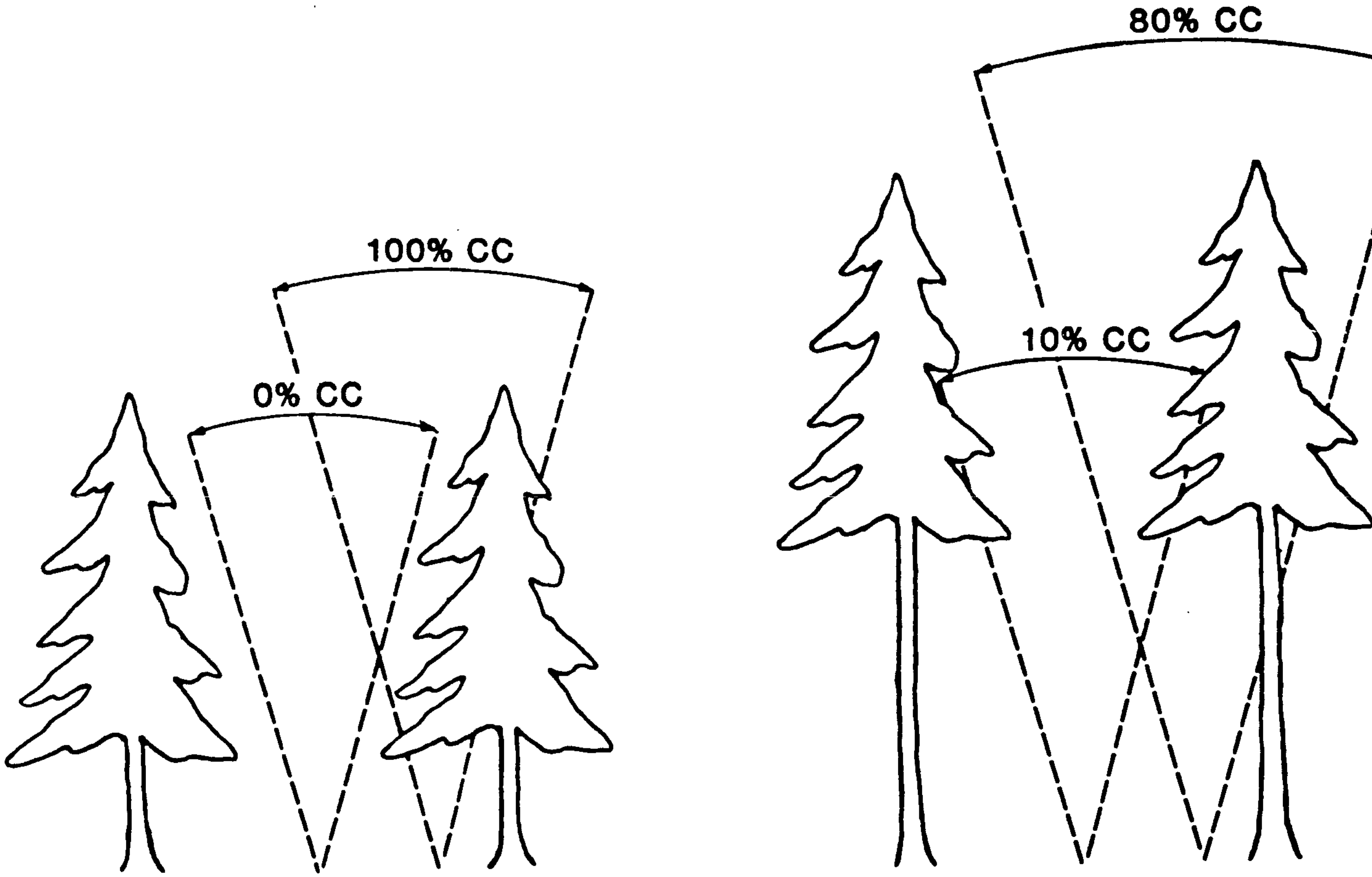


Figure 12. Schematic presentation of the relation between height to base of live crown and variance of the associated crown completeness estimates.

would be measured differently, for example, in a comparison of MCC between young forests with low HBLC and old-growth forests with higher HBLC (Fig. 12).

Table 2 and Figure 13 display crown completeness estimates for the forest stands in the three studies reported here. As would be expected with percentage data, the standard deviation of crown completeness measurements increases with decreasing crown completeness (Fig. 13). Lack of data in the lower crown completeness range prevented depiction of the complete binomial distribution as presented by Bonnor (1967) and Vales and Bunnell (1985).

Intra-stand crown completeness does not follow a normal distribution as is exemplified by the data from Mt. Seymour (Fig. 14). Despite the statistical artifact of percentage data, old-growth stands generally have lower MCC and higher intra-stand variance than 20 to 120-yr-old second-growth stands. Within all stands the cumulative frequency of measurements rises steeply within the range of 80-100% crown completeness. Generally, second-growth has approximately 70% of the measurements within this range. Typical old-growth stands are characterized by large, frequent openings which contribute to large 'steps' in the cumulative frequency of moosehorn readings (Fig. 14). The frequency curve is flatter with approximately 50% of the readings below 80%CC. It is expected, on the basis of the cumulative frequency of CC, that interception of snow is less in old-growth forests but that a wider range, higher

Table 2. Crown completeness (MCC) estimates as measured by the moosehorn technique for the Mt. Seymour and UBC Research Forest study sites.

Stand	Age (yrs)	MCC (%)	Standard deviation	No. of samples
UBCRF				
3 x 3 spaced 50% thinned	18-20	94	4.32	4
3 x 3 spaced 0% thinned	18-20	92	1.63	4
6 x 6 spaced	18-20	88	3.26	4
9 x 9 spaced	18-20	85	2.00	4
12 x 12 spaced	18-20	82	2.80	4
15 x 15 spaced	18-20	79	4.24	4
Nelder-south transect	18-20	69	7.09	7
Nelder-west transect	18-20	73	26.40	7
Nelder-east transect	18-20	92	5.54	7
Second-growth	60-80	94	19.68	78
Old-growth	> 150	87	25.16	65
Mt. Seymour				
Second-growth	80-85	83	32.24	60
Old-growth	> 150	72	23.50	60

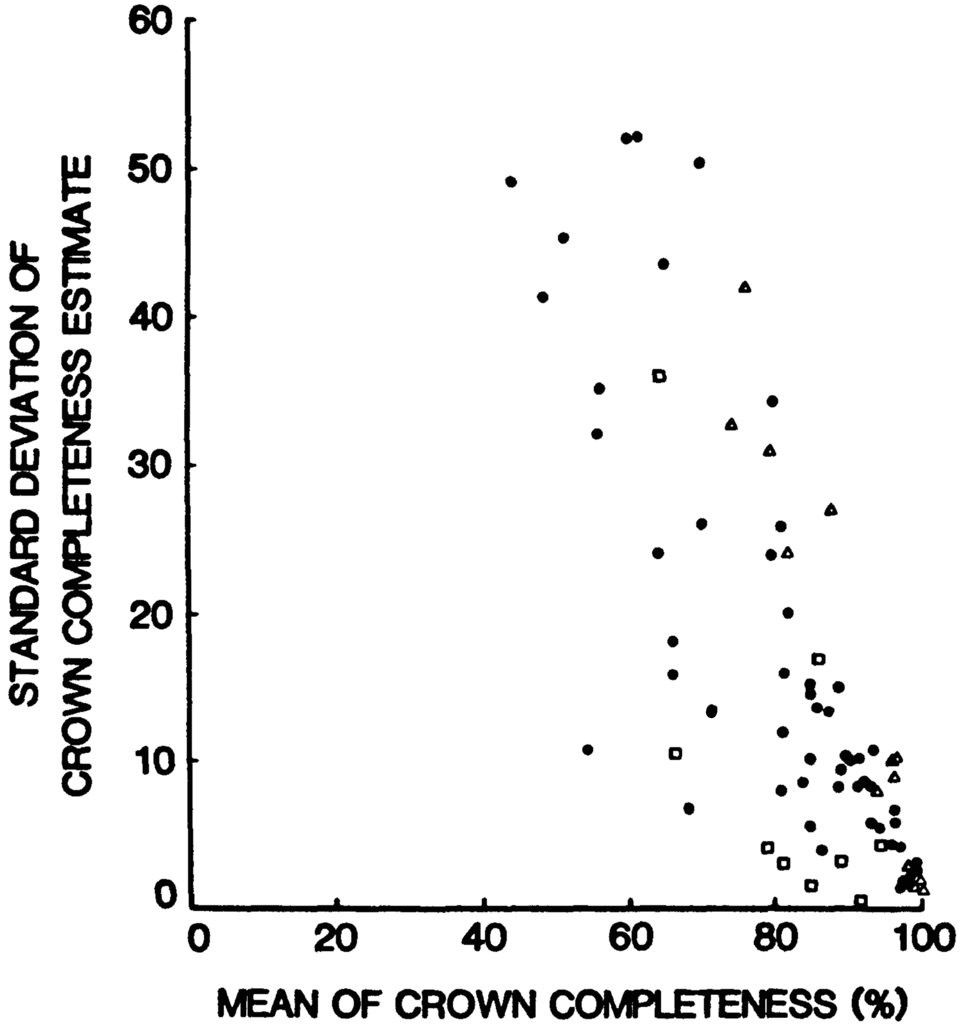


Figure 13. The relationship between standard deviation and mean of crown completeness estimates where data is from (△) UBC Research Forest study 1, (□) UBC Research Forest study 2, and (●) Mt. Seymour study.

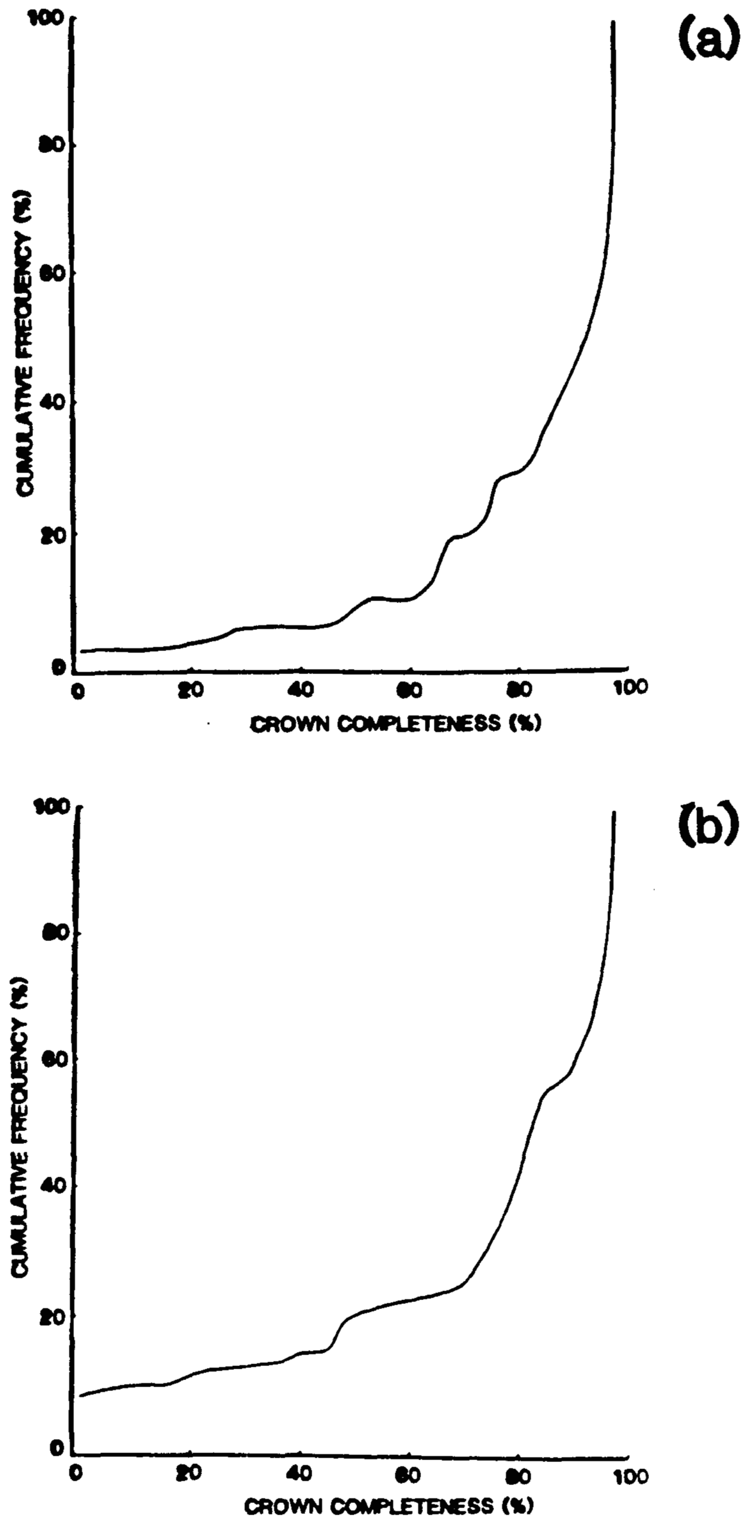


Figure 14. Cumulative frequency distribution of crown completeness measurements from a) an 80-year-old, second-growth forest and b) an old-growth forest on Mt. Seymour.

variance, and a different spatial distribution of snow depths occur.

Figure 15 displays cumulative frequency distributions of snow depth measurements taken from the same plots as the crown completeness data of Figure 14. Not only is the range of snow depth greater in the old-growth stand but an analysis of variance of depths reveals variance to be significantly greater ($P < 0.05$). Analysis of data on fresh snow provide the same results. Eighty percent of the snow depth measurements in the second-growth stand are within the narrow range of 20-45 cm reflecting the homogeneity of the canopy (Figs. 14 and 15). The same proportion of measurements in the old-growth stand represents a range of 20-90 cm. No snow depths occurred below 80 cm in the open plot which indicates that all snow depths were greater than deer chest height. The heterogeneity associated with both MCC and snow depths in old-growth forests is expected to provide a more optimal combination of forage availability (assuming that forage productivity responds to light) and ease of locomotion for deer when compared to the homogeneity of second-growth.

Table 3 summarizes data on snow depths collected from individual storms as well as from snowpacks. The sparse data do not allow analyses comparable to those for the snow water equivalents (Section 4.1.2). Nevertheless, trends for increasing interception with increasing storm size can be noted when canopy closure is held constant (Table 3 and Fig. 16).

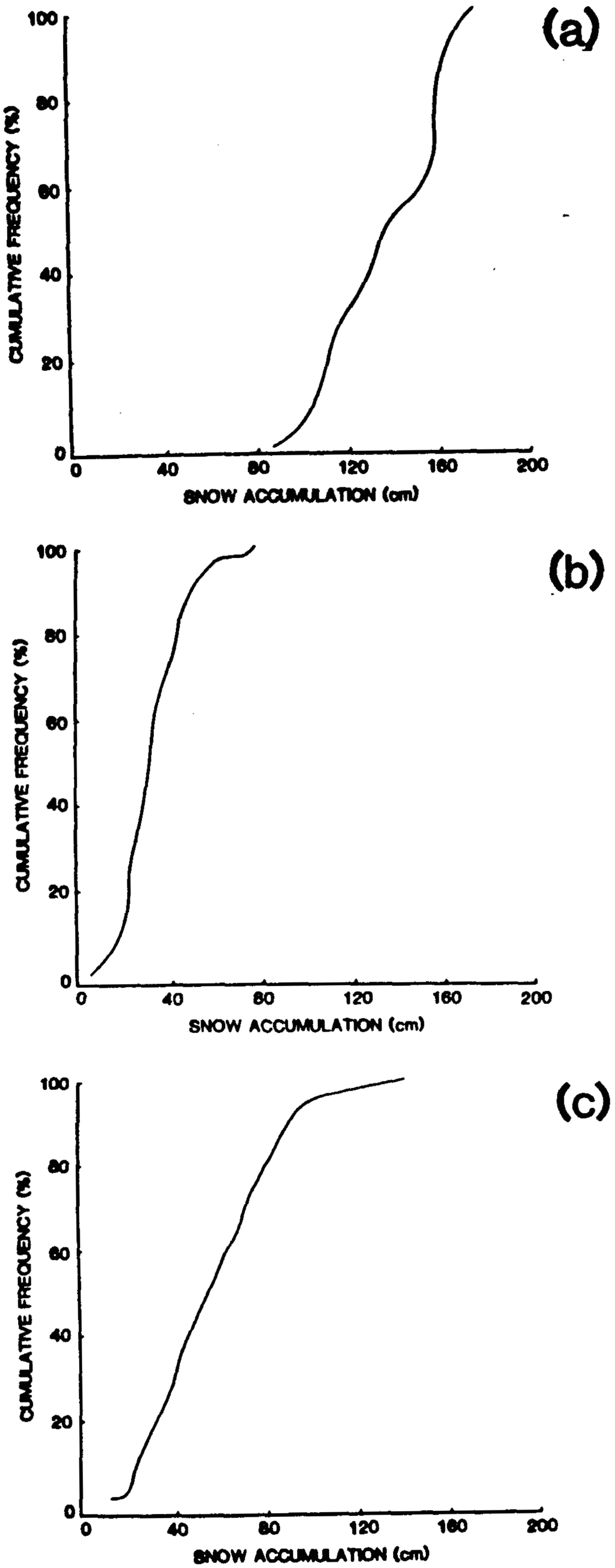


Figure 15. Cumulative frequency distribution of snow depth measurements from (a) open conditions, (b) an 80-year-old, second-growth forest, and (c) an old-growth forest on Mt. Seymour.

Table 3. Snow interception (depth) in stands during individual storms and for total snowpacks.

Location	Date	Stand type	MCC (%)	Snow depth (mm)			Interception (%)	Remarks
				Load	Under canopy	Open		
UBCRF	01.82	3 x 3 spaced	92	179.38	125.42	304.80	59	Individual storms
	01.82	Douglas-fir		144.27	66.84	211.11	68	
		18-20 yrs old						
	01.82	3 x 3 spaced	94	183.75	121.05	304.80	60	Individual storms
	01.82	50% thinned		149.48	61.63	211.11	71	
		Douglas-fir						
		18-20 yrs old						
	01.82	6 x 6 spaced	88	183.13	121.67	304.80	60	Individual storms
	01.82	Douglas-fir		141.28	69.83	211.11	67	
		18-20 yrs old						
	01.82	9 x 9 spaced	85	162.50	142.30	304.80	53	Individual storms
	01.82	Douglas-fir		141/49	69.62	211.11	67	
		18-20 yrs old						
	01.82	12 x 12 spaced	82	165.63	139.27	304.80	54	Individual storms
	01.82	Douglas-fir		142.50	68.61	211.11	68	
		18-20 yrs old						
	01.82	15 x 15 spaced	79	154.38	150.42	304.80	51	Individual storms
	01.82	Douglas-fir		138.33	72.78	211.11	66	
		18-20 yrs old						
	01.82	East nelder plot	93	199.82	104.98	304.80	66	Individual storms
	01.82	Douglas-fir		146.19	64.92	211.11	69	
		18-20 yrs old						
	01.82	West nelder plot	73	145.00	159.80	304.80	48	Individual storms
	01.82	Douglas-fir		88.57	122.54	211.11	42	
		18-20 yrs old						
	01.82	South nelder plot	69	154.41	150.39	304.80	51	Individual storms
	01.82	Douglas-fir		113.17	97.94	211.11	54	
		18-20 yrs old						

Mt. Seymour	01.84 01.84	80 yrs old Douglas-fir/ western red cedar	83	161.80 97.30	104.50 110.70	266.30 208.00	61 46	Individual storms
	01.84 01.84	> 200 yrs old Douglas-fir/ western red cedar	72	134.80 60.20	131.50 147.80	266.30 208.00	51 30	Individual storms
UBCRF	03-04.82	Cedar/Hemlock/ Douglas-fir ≈ 50 yrs old 525 m in elevation	97	665.30	124.74	790.04[1]	84	Snowpack measure
	03-04.82	Hemlock/Douglas- fir ≈ 80 yrs old 740 m in elevation	91	573-37	442-74	1016.11[1]	56	Snowpack measure
	03-04.82	Cedar/Hemlock > 200 yrs old 575 m in elevation	97	708.85	501.15	1210.00[1]	59	Snowpack measure
	03.04.82	Hemlock/Douglas- fir > 200 yrs old 730 m in elevation	81	336.16	675.51	1011.67[1]	33	Snowpack measure
Mt. Seymour	01.84	80 yrs old Douglas-fir/western red cedar	83	910.71	313.37	1224.08	74	Snowpack measure
	01.84	> 200 yrs old Douglas-fir/western red cedar	72	630.91	593.17	1224.08	52	Snowpack measure

1 Depths in open were not found to be significantly different ($P \geq 0.05$).

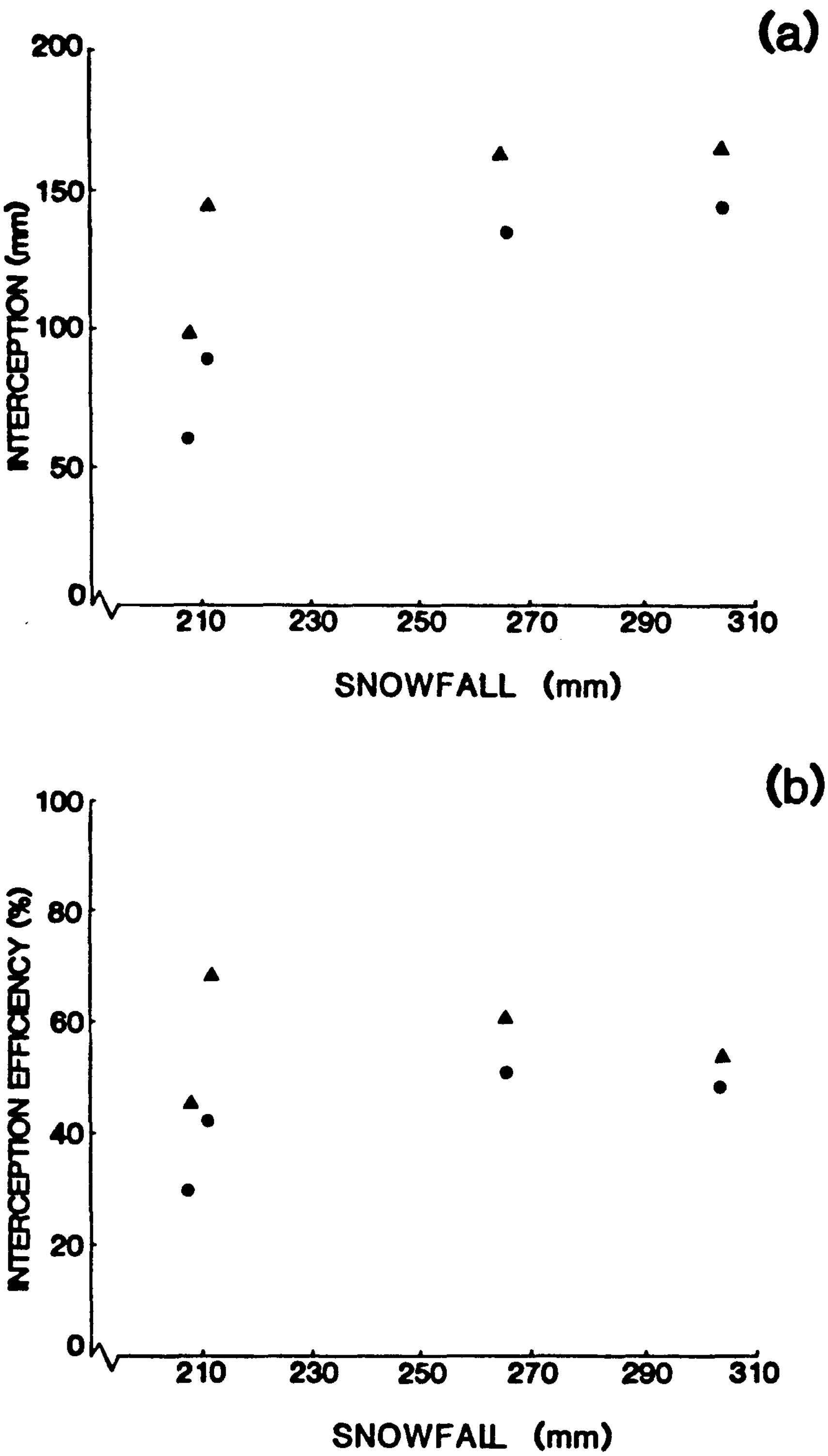


Figure 16. Snow interception (a) and interception efficiency (b) of two stands (crown completeness for second-growth was 83% (▲) and for old-growth, 72% (●)) as a function of storm size.

Interception appears to be asymptotic near storm sizes of 31 cm. Interception efficiency usually decreases as storm size increases, however, Figure 16b does not show this. Temperature is suspected of counfounding the results depicted in Figure 16 (Section 3.2). Data are stand mean values (MCC). Second-growth stands appear to be more efficient interceptors of snow as a result of their generally higher crown completeness.

With pooled data from Mt. Seymour and University of British Columbia Research Forest, interception (I) and interception efficiency (IE) both were found to be significantly related to canopy completeness as measured with the moosehorn (Eqs. 8 and 9, Fig. 17).

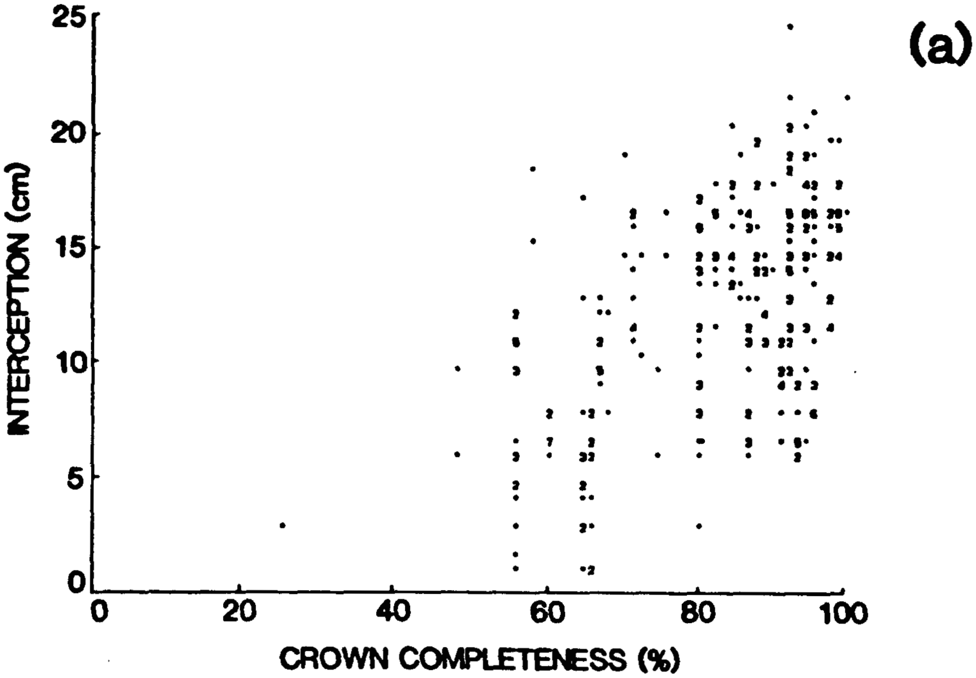
$$I(cm) = -2.14 + 0.174\ MCC \quad (8)$$

$$(n = 326,\ r^2 = 0.35,\ SE = 3.85,\ P \leq 0.0001)$$

$$IE = -1.345 + 0.617\ MCC \quad (9)$$

$$(n = 326,\ r^2 = 0.37,\ SE = 13.36,\ P \leq 0.0001)$$

The variation in interception efficiency measured at 100% crown completeness (Fig. 17) indicates that crown completeness as an index of snow interception is insufficient. Only 37% of the variation in interception efficiency can be explained by crown completeness. If crown completeness (measured by the moosehorn) is used as an independent variable to predict snow interception, it would best be viewed not as an estimate of the



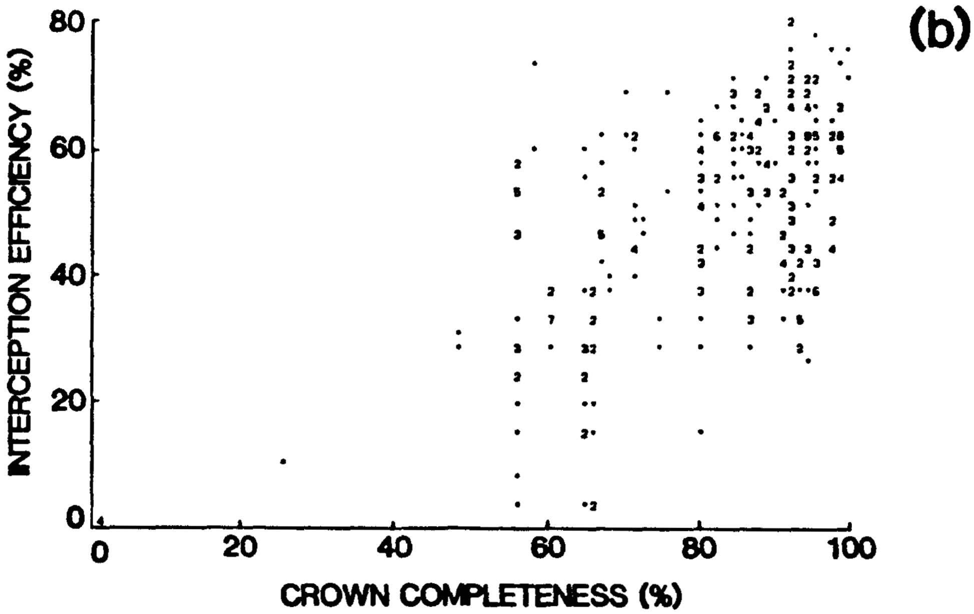


Figure 17. Snow interception (a) and interception efficiency (b) as a function of crown completeness.

intercepting surface, but as a lack thereof. Figure 18 (a, c, and d) schematically represents three stands of approximately equal crown completeness. The moosehorn would rank these three stands similarly in their ability to intercept snow whereas the intercepting surface areas are drastically different. The three stands (Fig. 18a, c, d) are more alike when one considers the potential for throughfall to occur (100-CC). Crown completeness is more correctly viewed as an index to throughfall (% open crown) which does not necessarily have any relationship to a stand's interceptive potential (compare Fig. 18a and b).

Interceptive ability of a stand is a three dimensional process. Canopy width and height estimates were computed to form an index of crown surface area (each crown was considered to be a cone). Individual estimates of crown surface area for each plot were multiplied by stocking estimates for each plot to obtain plot estimates of stand crown surface area (SCSA). The data suggest that interception efficiency is significantly related to stand crown surface area in a positive logarithmic function (Eq. 10 and Fig. 19).

$$IE = 25.38 + 5.76\ (\log SCSA) \qquad (10)$$

$(n = 20,\ r^2 = 0.30,\ SE = 3.75,\ P < 0.012)$

The relationship presented in Figure 19 is weak, particularly at the extreme low and high SCSA estimates. The calculations are based on average crown surface area estimates

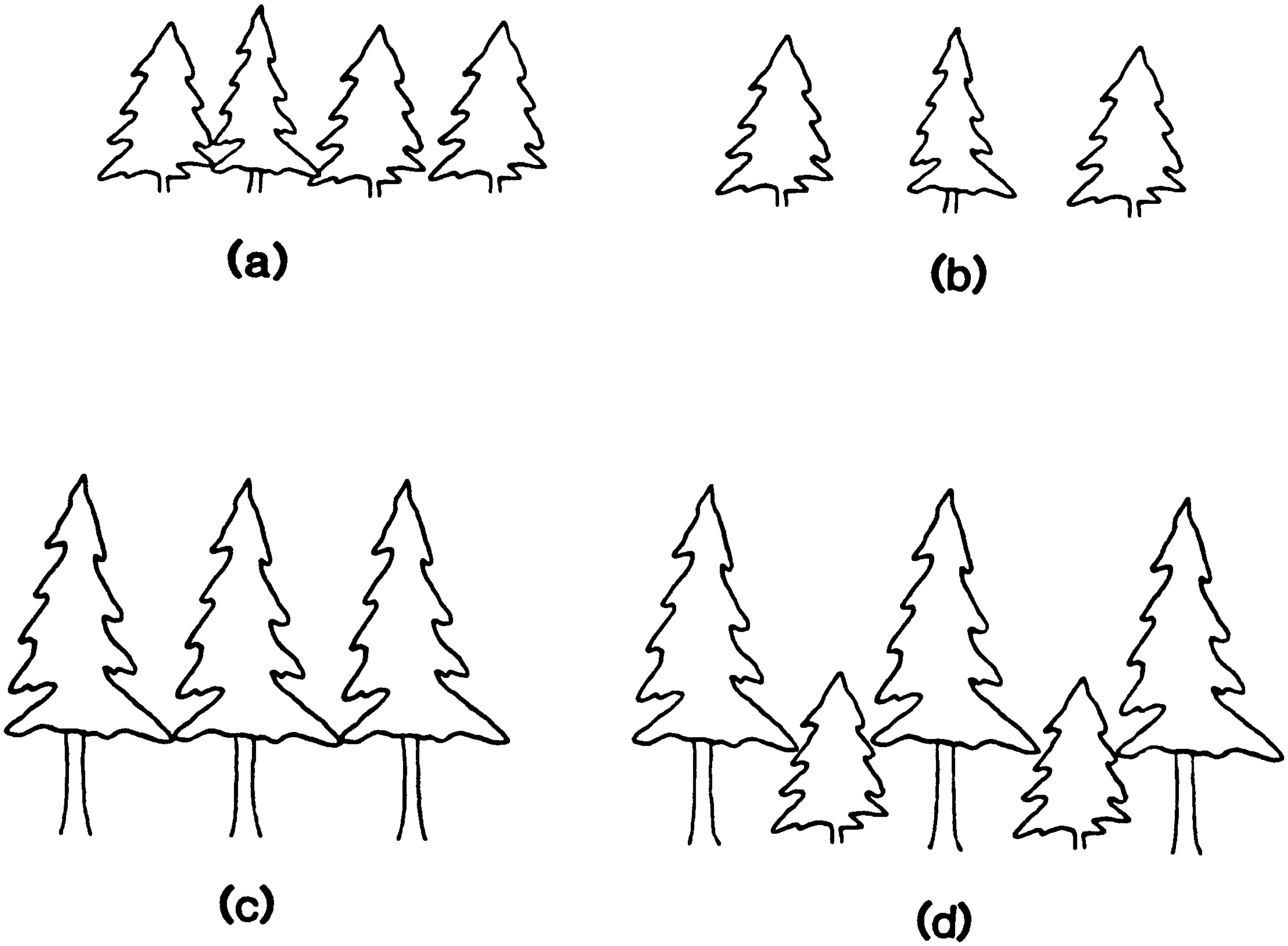


Figure 18. A schematic depiction of the conceptual differences between crown completeness (a and b) and interceptive surface (c and d)(see text for explanation).

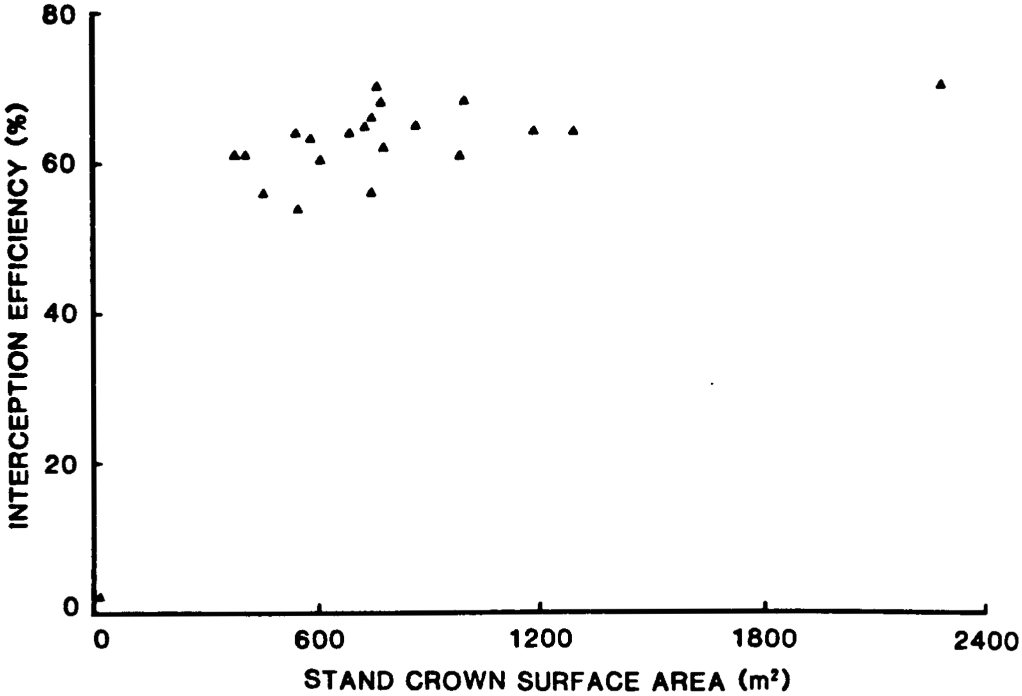


Figure 19. Forest snow interception efficiency as a function of average stand crown surface area.

per plot and average stocking estimates per plot. It would be desirable to obtain more precise estimates by measuring crown width and height estimates for each tree within sample plots. Such data could then be more appropriately evaluated regarding the suggested asymptotic shape and as an index to stand interceptive potential (Fig. 18).

Snowpacks.--No significant relationship was found between crown closure and apparent interception or apparent interception efficiency. These results indicate that other processes subsequent to snow interception significantly alter snowpack accumulation. In the warm maritime climate of coastal British Columbia, inter-storm ablation would be one plausible explanation.

4.1.2 Crown Completeness and Snow Interception: Snow Water Equivalent

Snow water equivalent measurements are the most frequently reported measures of snow accumulation in hydrology literature but cannot be considered equal to snow depths in cm. SWE measurements from Mt. Seymour snowpacks $\geq$ 7 cm in depth (n = 343) were divided by the average snow density (D) and regressed against the "actual" snow depth measured in cm to obtain the following equation:

$$S(\text{cm}) = 4.36 + 0.97 \frac{SWE}{D} \qquad (11)$$
$$(n = 343,\ r^2 = 0.97,\ SE = 6.78,\ P \leq 0.001)$$

The equation is valid provided that some estimate of average snow density is available. Fitzharris (1975) reported that snow density is predictable but depends largely upon region or location (maritime or continental) as well as the time of year (early winter or late winter). Although the subsequent analyses will use snow depth in SWE, the resultant SWE data from prediction equations could be transformed, using equation 11 and snow densities for coastal climates, to cm units (e.g., Appendices I and II - models ISWE and SSWE).

Snow water equivalent measurements should increase the predictive power of interception efficiency relationships with crown completeness because the influence of melt will not confound the relationship until snowpack saturation occurs. The superiority over depth in cm units should be especially evident when considering apparent interception efficiency and total snowpack measures.

Single Storms.--Table 4 summarizes available data on intercepted snow (measured in SWE) in stands during single snow storms. The available data indicate that the amount of snow held in stand canopies tends toward a positive linear relationship with increasing precipitation over a considerable range of precipitation. Data from Table 4 are presented in Figure 20. No tendency towards an upper asymptote to snow load

Table 4. Snow interception (SWE) in stands during individual storms (adapted from Bunnell et al. 1984).

Source and location	Date	Stand type	MCC (%)	Snow water equivalent (cm) Interception	Under canopy	Open	Interception efficiency (%)	Remarks
Munns (1921)		Jack pine	80	0.03	0.00	0.03	100	Mean of several storms.
in U.S. Army				0.04-0.09	0.01-0.04	0.05-0.13	77	Refers to mixed rain and
(1956);				0.11-0.24	0.04-0.06	0.15-0.25	75	snow converted from SWE
California				0.11-0.30	0.17-0.46	0.28-0.76	38	(inches).
				0.33	0.46-0.74	0.79-1.27	42	
					0.96-1.86	1.30-2.51	26	
					2.00-3.96	2.57-5.08	25	
					3.88	5.11+	24	
Maule (1934)	12.10	Hardwood; 3	100	0.51	2.54	3.05	17	Snow values extracted
Connecticut	12.13	age classes		0.25	3.81	4.06	6	from his Figure 1. Snow
	12.17	(1-20, 20-40,		0.00	13.21	13.21	0	from individual storms
	01.29	40-60 yrs);		0.00	2.03	2.03	0	was measured. Snow
	02.04	6.1-19.8 m		2.54	3.05	5.59	45	measured in inches depth
	02.11	in height		0.00	17.27	17.78	3	and transformed here on
								the basis of a density
	12.10	Red pine;	9-14	2.03	1.02	3.05	67	of 0.1 $gm \cdot cm^{-3}$.
	12.13	7.3 m in		2.54	1.52	4.06	63	
	12.17	height;		7.11	6.10	13.21	54	
	01.29	11-20 yrs		0.51	1.52	2.03	25	
	02.04			3.05	2.54	5.59	55	
	02.11			4.32	13.46	17.78	24	
	12.10	Norway	6-7	2.29	0.76	3.05	75	
	12.13	spruce; 9.1		2.79	1.27	4.06	69	
	12.17	m in height;		8.64	4.57	13.21	65	
	01.29	11-20 yrs		1.01	1.02	2.03	50	
	02.04			4.32	1.27	5.59	77	
	02.11			8.13	9.65	17.78	46	
	12.10	White pine;	5	1.53	1.52	3.05	50	
	12.13	7.9 m in		3.04	1.02	4.06	75	
	12.17	height; 11-20		6.86	6.35	13.21	52	
	01.21	yrs		0.76	1.27	2.03	38	
	02.04			3.05	2.54	5.59	55	
	02.11			2.54	15.24	17.78	14	

	12.10	Hemlock;	12-13	1.14	1.91	3.05	38	
	12.13	14.6-21.3		2.15	1.91	4.06	53	
	12.17	m in height;		6.86	6.35	13.21	52	
	01.29	uneven age		0.76	1.27	2.03	38	
	02.04			3.05	2.54	5.59	55	
	02.11			4.32	13.46	17.78	24	
Johnson (1942) Colorado		Ponderosa pine		0.76-1.27				13 rainstorms analyzed. It is suggested on no evidence that maximal rain load is equal to maximal snow load.
Morey (1942)	04.11	Hardwood; fully stocked		2.03		20.83	10	Measured after snow had blown off.
Vermont	04.11	60-yr-old spruce;		9.14		20.83	44	
	04.11	30-yr-old		9.14		20.83	44	
Kittredge	Winters	White fir;	51	0.43	0.57	1.00	43	110 storms measured; no
(1953)	of	mature 140 yrs		0.48	1.52	2.00	24	upper limit to interception
California	1934-38			0.63	4.37	5.00	13	although some cryptic
	and			1.31	13.87	15.00	7	comments about y-intercept
	1940-41							being "snow storage". Data
		Ponderosa	35	0.33	0.67	1.00	33	are computed from his
		pine; mature		0.43	1.57	2.00	21	regression equations p.9.
				0.73	4.27	5.00	15	Canopy cover is average
				1.73	13.27	15.00	12	within 6.1 m of station.
		Ponderosa	40	0.14	0.86	1.00	14	
		pine; 4.27 m		0.25	1.76	2.00	12	
				0.58	4.42	5.00	12	
				1.68	13.32	15.00	11	
		Red fir	75	0.89	0.11	1.00	89	
				1.02	0.98	2.00	51	
				1.41	3.59	5.00	28	
				2.71	12.29	15.00	18	
		White fir;	70	0.83	0.17	1.00	83	
		pole size		1.00	1.00	2.00	50	
				1.51	3.99	5.00	20	
				3.21	11.79	15.00	21	

		Mixed	55	0.88	0.13	1.00	87	
		conifer;		1.12	0.88	2.00	56	
		cutover		1.84	3.16	5.00	37	
				4.24	10.76	15.00	28	
		Sugar/	62	0.53	0.47	1.00	53	
		ponderosa		0.81	1.19	2.00	41	
		pine		1.65	3.35	5.00	33	
				4.45	10.54	15.00	30	
Strobel	01.06	uneven-aged	61	1.15	1.29	2.44	47	Data are for individual
(1978)	01.14	coniferous;		0.45	0.86	1.31	34	storms.
Alp	01.16	29.3 m^2/ha		0.88	0.53	1.41	62	
mountains	01.18			1.77	2.20	3.97	45	
	01.22			1.39	4.14	5.53	25	
	01.28			2.05	8.02	10.07	20	
	01.06	uneven-aged	86	1.25	1.16	2.41	52	
	01.14	coniferous;		0.90	0.67	1.57	57	
	01.16	75.1 m^2/ha		0.85	0.48	1.53	69	
	01.18			1.76	2.27	4.03	44	
	01.22			2.45	3.70	6.15	40	
	01.28			3.33	7.47	10.80	31	
Rowe and	1940-	Ponderosa	40	0.13	1.27	1.40	9	Data are for storms
Hendrix	1946	pine; 65-70		0.25	1.40	1.65	15	(> 1.0 cm SWE) in which
(1951)		yr-old; 1450		0.38	1.65	2.03	19	$\geq$ 50% of precipitation
California		trees/ha;		0.39	1.90	2.29	17	fell as snow. No evidence
		6.7-33.8 m in		0.50	2.29	2.79	18	of upper limit to
		height;		0.76	2.16	2.92	26	interception.
		elevation 1005 m		0.25	2.67	2.92	9	
				0.89	2.29	3.18	28	
				0.38	2.92	3.30	31	
				0.51	3.05	3.56	14	
				0.38	3.30	3.68	10	
				0.26	3.68	3.94	7	
				0.51	3.81	4.32	12	
				0.38	4.06	4.44	9	
				0.76	3.81	4.57	17	
				0.77	4.06	4.83	16	
				0.38	4.57	4.95	8	
				1.02	4.57	5.59	18	

				0.64	5.08	5.72	11	
				0.76	6.22	6.98	11	
				0.77	6.98	7.75	10	
				1.01	7.37	8.38	12	
				1.26	9.14	10.40	12	
				1.02	10.41	11.43	9	
				2.16	13.46	15.62	14	
				1.01	15.88	16.89	6	
				2.67	20.70	23.37	11	
				3.68	26.42	30.10	12	
Fitzharris (1975) Coastal B.C.	1969-1971	Mixed conifer; elevation 590 m	51	0.10	0.10	0.30	67	82 individual storms were measured. Data here represent a subset of his data chosen for a range of canopy closures and snow storm sizes.
				1.90	1.40	3.30	18	
				3.50	3.90	7.40	7	
				0.10	0.00	0.10	100	
				0.20	0.00	0.20	100	
				0.30	0.00	0.30	100	
		Mixed conifer; elevation 710 m	91	0.03	0.00	0.30	100	
				3.50	1.00	4.50	98	
				1.50	7.80	9.30	16	
				0.20	0.00	0.20	100	
				0.80	0.20	1.00	80	
				2.00	0.60	2.60	79	
		Mixed conifer; elevation 790 m	71	0.30	0.20	0.50	60	
				2.90	7.70	10.60	27	
				2.55	2.35	4.90	52	
				0.20	0.00	0.20	100	
				1.10	0.60	1.70	65	
				2.9	0.70	3.60	80	
		Mixed conifer; elevation 1060 m	29	0.30	0.00	0.30	100	
				0.80	6.60	7.40	11	
				5.00	9.90	14.90	34	
				0.30	0.00	0.30	100	
				3.00	1.00	4.00	75	
				6.40	1.70	8.10	79	

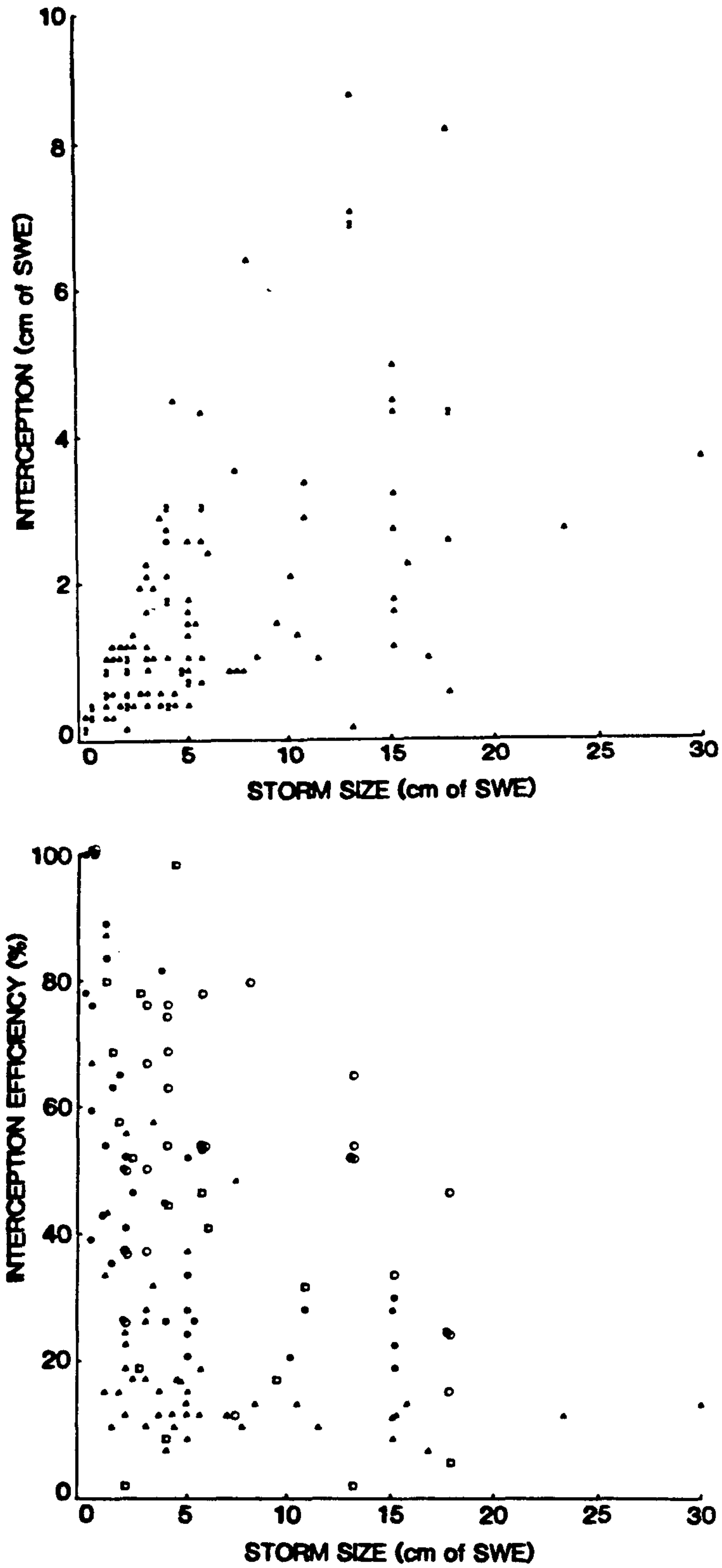


Figure 20. Snow interception (a) and interception efficiency (b) in stands during individual storms of different sizes where (○=0-30%, ▲=31-60%, ●=61-80%, and □=81-100%) are estimates of mean crown completeness.

is noted (Fig. 20a).

A number of explanations for the absence of a clear asymptote are plausible:

1) Snow is blowing or falling off the canopy and being redeposited in the open. Redistribution would increase the apparent snowfall without increasing snow under the canopy.

2) Significant amounts of snow are melting in the canopy and dropping off.

3) Significant amounts of snow are sublimating or melting and being evaporated.

4) Adjacent trees are interacting in some manner (i.e., interlocking branches) so that greater snow loads can be held.

The premise that snow in the open equals true snowfall and that snow in the open minus snow under the canopy equals snow interception is unlikely to be wholly correct. If individual trees in a stand were each weighed during snow storms which were accurately measured by gauges positioned above the canopy, there seems little doubt that maximal snow loads could be measured for stands (e.g., Fig. 6). Kittredge, in his pioneering work, and many others after him simply assumed that intercepted snow sublimates rapidly. Figure 21 offers a first approximation to the effects of storm size on interception by reanalyzing data of Kittredge (1953). The data from Table 4 (Fig. 20b) depict similar patterns to those found by Kittredge (Fig. 21). The same general tendency exists for decreasing interception efficiency with increasing storm size. The function decreases less sharply at higher crown completeness which also indicates that a unit of canopy is more efficient at higher snowfalls than in lower snowfalls.

Within the data of Kittredge (1953) there also is no asymptote for snow load versus increasing storm size which would relate to maximal interception (Table 4). All of Kittredge's regression equations are linear, however, this result may be because the large variance precluded other interpretations of the data. Figure 22 presents percent interception as a function of crown completeness for various storm sizes. With increasing storm size, the slope decreases. The broad pattern is similar to that of interception efficiency discussed in Section 1.3.

<u>Snowpacks</u>.--Clearly, any attempt to predict percent interception by canopy measures alone is not appropriate; a storm size component must be included:

$$AIE = f(A, MCC) \qquad (12)$$

where AIE = apparent interception efficiency (%), MCC = mean

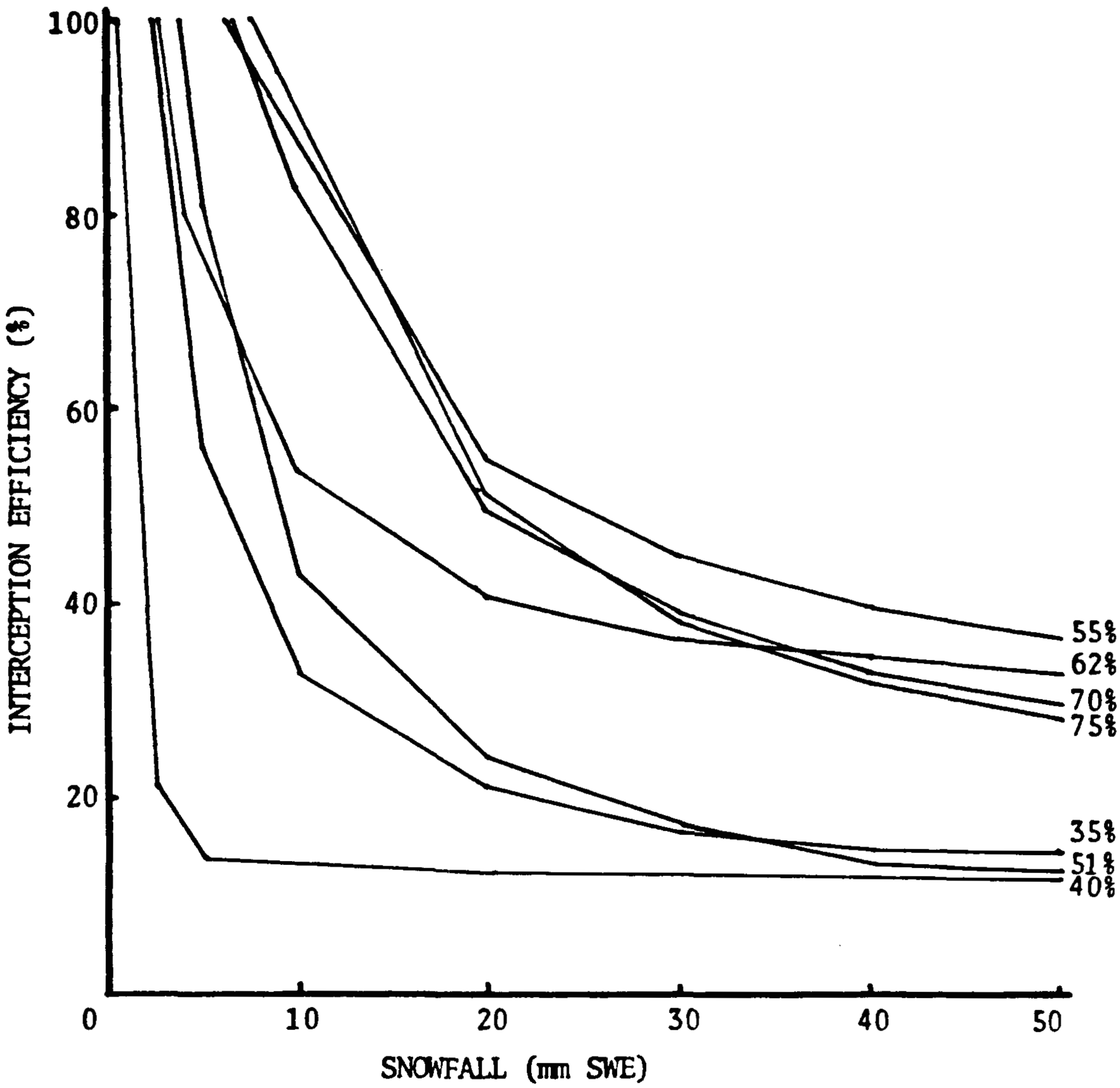


Figure 21. Effect of storm size on interception efficiency. Percentages are measurements of mean crown completeness (derived from equations of Kittredge 1953: 9, from Bunnell *et al*. 1984: 351).

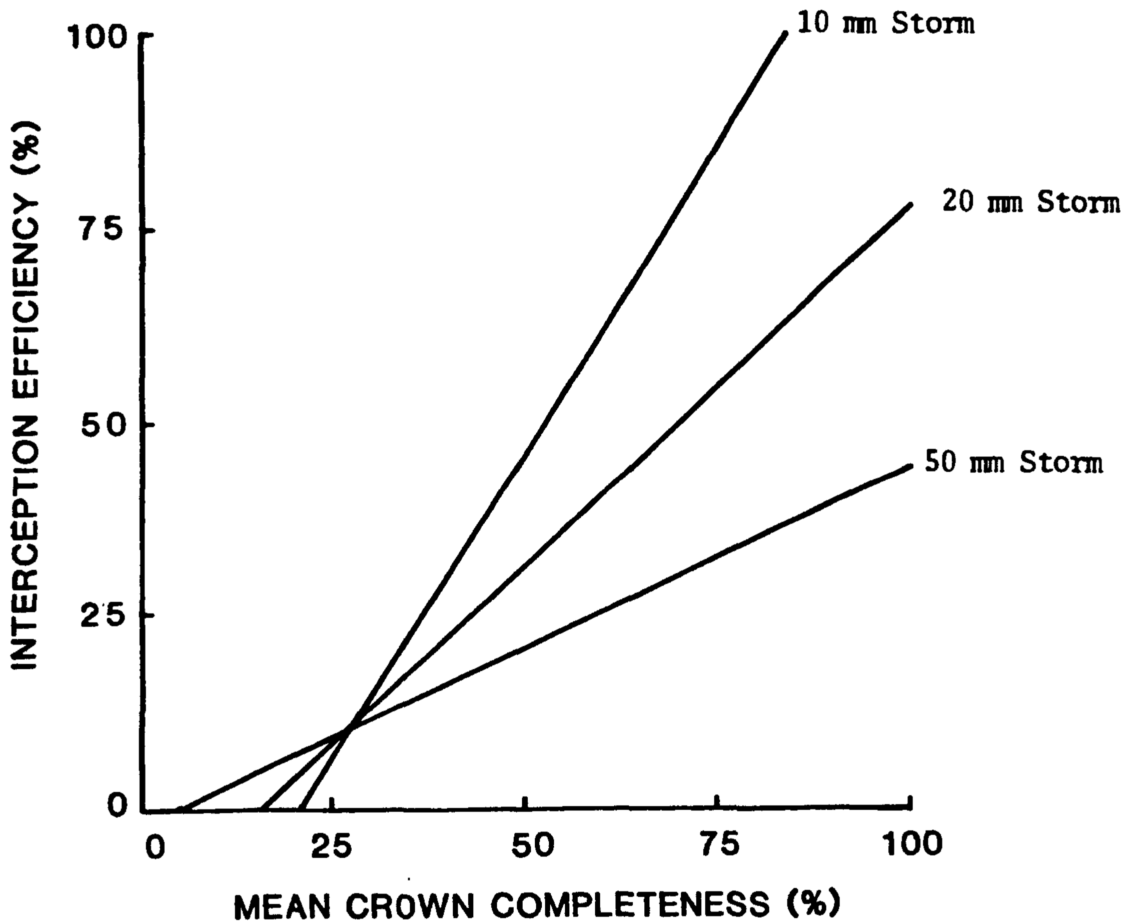


Figure 22. Effect of mean crown completeness on percentage interception for various storm sizes (derived from data of Kittredge 1953: 9, from Bunnell et al. 1984: 352).

crown completeness (%), and A is some storm size function. Harestad and Bunnell (1981) suggested that A can be described by a function incorporating the slopes of relative SWE (SWE in forests/SWE in open *100) and MCC regressions for various snow regimes. The relative SWE is assumed to reflect a canopy's AIE and on a relative basis allows interstudy treatment of the data. The analysis is much similar to working with stand means and similarly allows trends to be depicted clearly. Therefore:

$$AIE = 100 + A(MCC) \text{ and} \tag{13}$$

$$A = a + b\ S(m) \tag{14}$$

where S(m) = maximum snow water equivalent in open and A = slope of regression between apparent interception efficiency and mean crown completeness.

The regression resulting from the data that Harestad and Bunnell (1981) presented is strongly linear:

$$A = -1.51 + 0.015\ S(M) \tag{15}$$

$$(n = 13,\ r^2 = 0.82,\ SE = 0.19,\ P < 0.0001)$$

Slopes of the regressions (Eq. 13) are strongly negative at low snow accumulations and weakly negative at higher snow accumulations.

Snowpack data of Fitzharris (1975), as well as snowpack data collected at the University of British Columbia Research Forest and Mt. Seymour, were added to those collated by Harestad and Bunnell (Table 5). The maximum snow water equivalent is the maximum observed during the winter. Fitzharris' data from high elevation areas (1060 m - 1260 m) with large snow accumulations are particularly curvilinear (Fig. 23). The curvilinear relationship suggests rapidly increasing importance of a given unit of crown completeness to interception as snowfall increases. That suggestion contradicts the general trend shown by the rest of Fitzharris' data (Table 5 and Eq. 3 and 4). A plausible explanation is revealed when it is noted that Fitzharris' high elevation data were from the dry snow zone where MCC was only 9 to 29%. The potential for mass transport of intercepted snow into open areas is high thereby biasing interception estimates upwards (see Section 3.2).

In regions of low snow accumulation (low S[m]) it is reasonable to assume that snowfalls are infrequent with relatively little snow deposited. Interception efficiency is thus consistently high (Fig. 23). In regions where frequent intense storms are expected, interception efficiency is lower (Fig. 8).

The analysis here agrees with Harestad and Bunnell (1981) who noted that with more data the relationship could prove to be slightly curvilinear. The reanalysis using the larger data base (but omitting Fitzharris' high elevation data) revealed a positive logarithmic function:

Table 5. Effects of forest crown completeness on maximum snow water equivalents (adapted from Harestad and Bunnell 1981).

Forest type	Stand age	Canopy closure (%)	Location	Elevation m	Slope of relative SWE canopy cover regression	Maximum SWE in open cm	Reference
Mixed hardwood and conifer	Saplings to sawtimber		New York	458-518	-0.30	27.2	Lull & Rushmore 1961
Lodgepole pine	-		Montana	High	-0.24	67.3	Farnes 1971
White pine	Various ages		Idaho	824-1678	-0.24	79.5	Packer 1962
Ponderosa pine	All ages		California	1525-1982	-3.12	4.1	Kittredge 1953
Ponderosa pine	All ages		California	1525-1982	-1.39	18.3	Kittredge 1953
White fir	140 years, mature		California	1525-1982	-0.70	50.8	Kittredge 1953
Red fir	200 years		California	1525-1982	-0.76	36.8	Kittredge 1953
Douglas-fir	Old growth & selectively logged		Oregon and Washington	503-534	-0.37	68.6	Kittredge 1953 (re-analysis of Hale 1950)
Mixed conifers	All ages		California	1525-1982	-1.20	12.7	Kittredge 1953
Mixed conifers	All ages		California	1525-1982	-0.93	38.1	Kittredge 1953
Mixed conifers	All ages		California	1525-1982	-1.05	53.1	Kittredge 1953
Mixed conifers	All ages		California	1525-1982	-1.33	24.9	Kittredge 1953
Mixed conifers	All ages		California	1525-1982	-0.52	83.0	Kittredge 1953
Mixed conifers	All ages		California	1525-1982	-1.43	7.1	Kittredge 1953
Mixed conifers	All ages		California	1525-1982	-1.08	21.1	Kittredge 1953

Western hemlock & yellow cedar	Mature	09	British Columbia	1260	-5.17	243	Fitzharris 1975
Western hemlock & yellow cedar	Mature	09	British Columbia	1260	-6.17	90	Fitzharris 1975
Western hemlock & yellow cedar	Mature	29	British Columbia	1060	-1.63	207	Fitzharris 1975
Western hemlock & yellow cedar	Mature	29	British Columbia	1060	-1.39	69	Fitzharris 1975
Western hemlock & yellow cedar	Mature	64	British Columbia	970	-0.36	130	Fitzharris 1975
Western hemlock & yellow cedar	Mature	64	British Columbia	970	-0.81	25	Fitzharris 1975
Western hemlock & yellow cedar	Mature	69	British Columbia	870	-0.65	78	Fitzharris 1975
Western hemlock & yellow cedar	Mature	71	British Columbia	790	-0.55	82	Fitzharris 1975
Western hemlock & yellow cedar	Mature	91	British Columbia	710	-0.48	60	Fitzharris 1975
Douglas-fir & western hemlock	60 years	97	British Columbia	525	-0.72	32.7	UBCRF data
Douglas-fir & western hemlock	80 years	91	British Columbia	740	-0.42	35.2	UBCRF data
Douglas-fir & western hemlock	120+ years	81	British Columbia	725	-0.36	41.2	UBCRF data
Douglas-fir & western hemlock	120+ years	97	British Columbia	580	-0.66	50	UBCRF data
Douglas-fir & western hemlock	120+ years	73	British Columbia	970	-0.75	59.7	Mt. Seymour data
Douglas-fir & western hemlock	80 years	82	British Columbia	970	-0.91	59.7	Mt. Seymour data

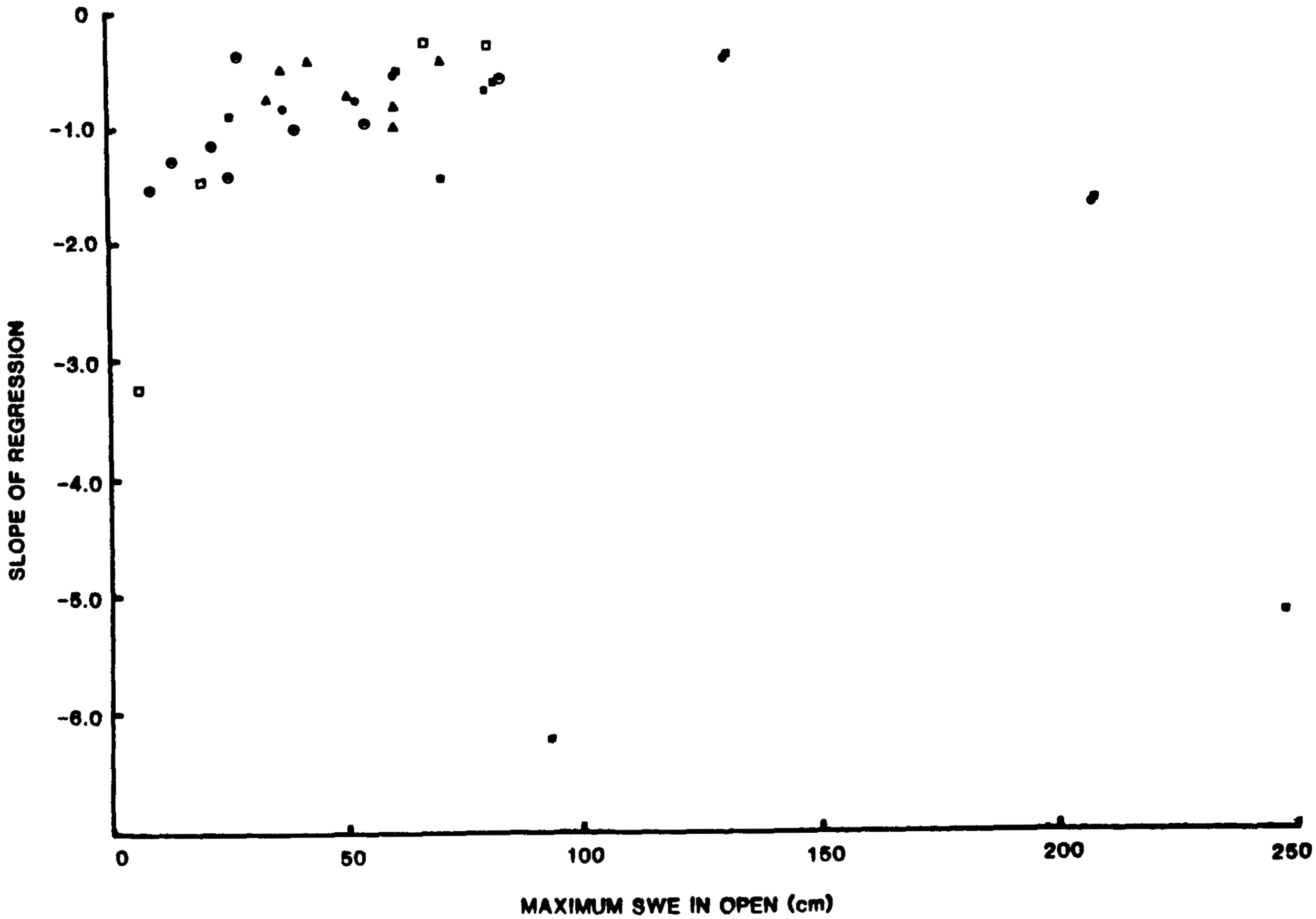


Figure 23. Slope of SWE-MCC regression as a function of maximum SWE in open. SWE used in the regression is the relative SWE (SWE in forest/ SWE in open X 100). Symbols represent mixed hardwood (○), mixed softwood (⊙), Douglas-fir and western hemlock (▲), western hemlock and yellow cedar (■), true fir (●), and pine (□) forest types.

$$A = -3.1 + 0.619 \, \mathrm{Ln} \, [S(m)] \qquad (16)$$

$(n = 25, r^2 = 0.72, SE = 0.32, P \leq 0.0001)$

Apart from the change in shape of the relationship the general conclusion is still that mean crown completeness integrates age and species characteristics well, and can be used to predict snow water equivalent in coniferous forests. Since AIE and S(m) are SWE measurements from total snowpacks, the relationship must also integrate inter-storm ablation. The same approach outlined by Harestad and Bunnell (1981) was applied to Table 4 where the data were SWE measurements but from individual storms. No significant relationship was found (Eq. 17).

$$A = -1.8 -0.0049 \, [S(m)] \qquad (17)$$

$(n = 130, r^2 = 0.0009, SE = 3.0245, P \geq 0.91)$

4.2 Implications for the Management of Coastal Forest Deer Winter Ranges

Three snow interception models were developed with the objective of identifying potential research and/or management actions that could alleviate concern over the provision of black-tailed deer winter habitat. Thus all modelling approaches were directed toward simulation of the combined effects of forest canopy interception of snow and the resultant snowpack effects on deer energetic expenditures for locomotion. Energy expenditure for locomotion is expressed as a function of deer sinking depth and snow density (g/cm^3). Sinking depth is expressed as a function of snow depth, surface hardness or supportability (g/cm^2), and snow density (g/cm^3). Snow depth is expressed as a function of forest canopy attributes (MCC and SCSA or just MCC) and magnitude of snowfalls or snow accumulations. Simulation modelling was chosen because it requires the explicit description of the relevant ecological processes in a logical language. The explicit statements further allow recognition of assumptions and make the conceptual model of perceived interactions less ambiguous. Modelling allows the development of a sense of which processes and parameters might be most important. The conceptual flow of a general model is presented in Figure 24.

At least four basic approaches could be adopted for modeling snow interception by forest canopies.

The basic approaches are identified by how the dependent variable (IE or AIE) is measured: i) from individual storms (models IDEPTH and ISWE), or ii) from total snowpacks (model SSWE).

Regardless of the approach and the inherent generality implicit in Figure 24, all models presented integrate many site variables and therefore become site specific. Most processes expressed by mathematical equations in the models are based on empirical data and should not be expected to hold precisely for conditions outside the range occurring during sampling.

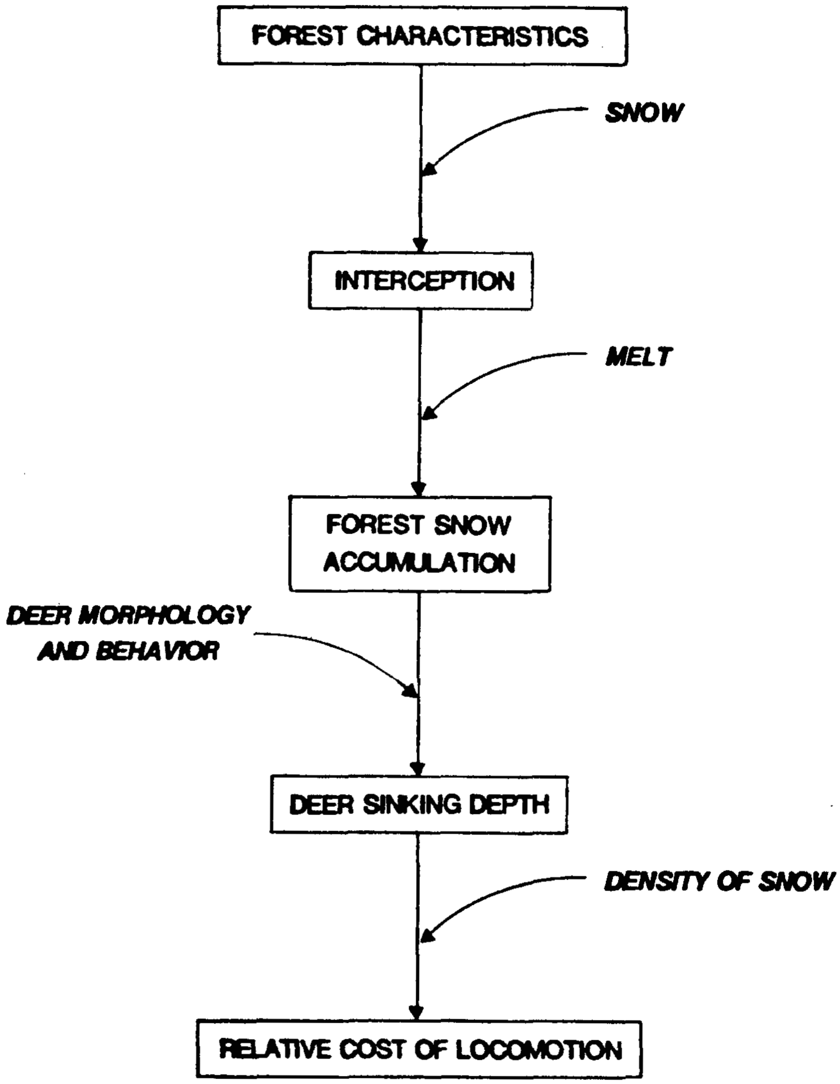


Figure 24. A generalized flow chart for the simulation models of snow interception and deer energetic expenditure.

Specific restrictions are noted in the following discussion.

4.2.1 "Individual Storm" Interception Models

A simulation of winter storm-to-storm dynamics with IE expressed as a percentage of snow depth in cm would be the best model to meet objectives concerning the implication of snow depth on deer locomotion (see Fig. 1, Appendix I). Such a model would allow evaluation of winter severity and would allow for precise estimates of snowpack development (e.g., inclusion of inter-storm melt periods, rain on snow events, etc.). Also, the dependent variable is in the appropriate units for investigating the effects of snow on deer locomotion (i.e., cm depth).

A model incorporating two forest variables (canopy completeness and stand crown surface area) was built to explore the relative effects on snow interception (Appendix I). The acronym IDEPTH was chosen to reflect the nature of the interception relationship used in this model - Individual storms with snow DEPTH.

Both models based on SWE interception data (ISWE presented here and SSWE presented in Section 4.2.2) transform SWE measurements to cm depth data utilizing equation 11. The transformation assumes that data are available to compute an average density for a snowpack in a given location.

Snow Interception.--The snow interception equation used in IDEPTH is a multiple linear regression equation utilizing data collected at the UBC Research Forest study (Table 2, Appendix I). Mean canopy completeness and stand crown surface area are the independent variables. No storm size information was available for the data used in this model and therefore IE was assumed to be linearly related to storm size.

The data indicate that the interception efficiency of a forest stand is more sensitive to crown completeness than to crown surface area (Fig. 25). The data apply only to the limited empirical situation of 18 to 20-year-old stands and snowfalls of a 30 cm magnitude. A 100% complete canopy with 100 m^2 surface area would intercept only 75% of a 30 cm storm (Fig. 25). Assuming a snow density of 0.3 g/cm^3, this estimate of interception efficiency is remarkably similar to that estimated by the ISWE model (see Fig. 26).

The interception model ISWE uses data of Fitzharris (1975) from Mt. Seymour (Fig. 26). Interception efficiency is calculated as a function of snowfall magnitude (Eq. 2) and adjusted linearly with MCC. MCC for Equation 2 was 51% (n = 175, s = 28.0). The model indicates that light snowfalls characterized by one cm SWE could be totally intercepted by forests with MCC $\geq$ 60%. Storms greater than 3 cm SWE could never be totally intercepted. The maximum storm size recorded by Fitzharris was 15 cm SWE. A forest with 100% MCC could intercept 75% of such a snowfall.

Deer Sinking Depth.--The mathematical formulation of deer sinking depth (Table 2, Appendix I, II) is limited empirically

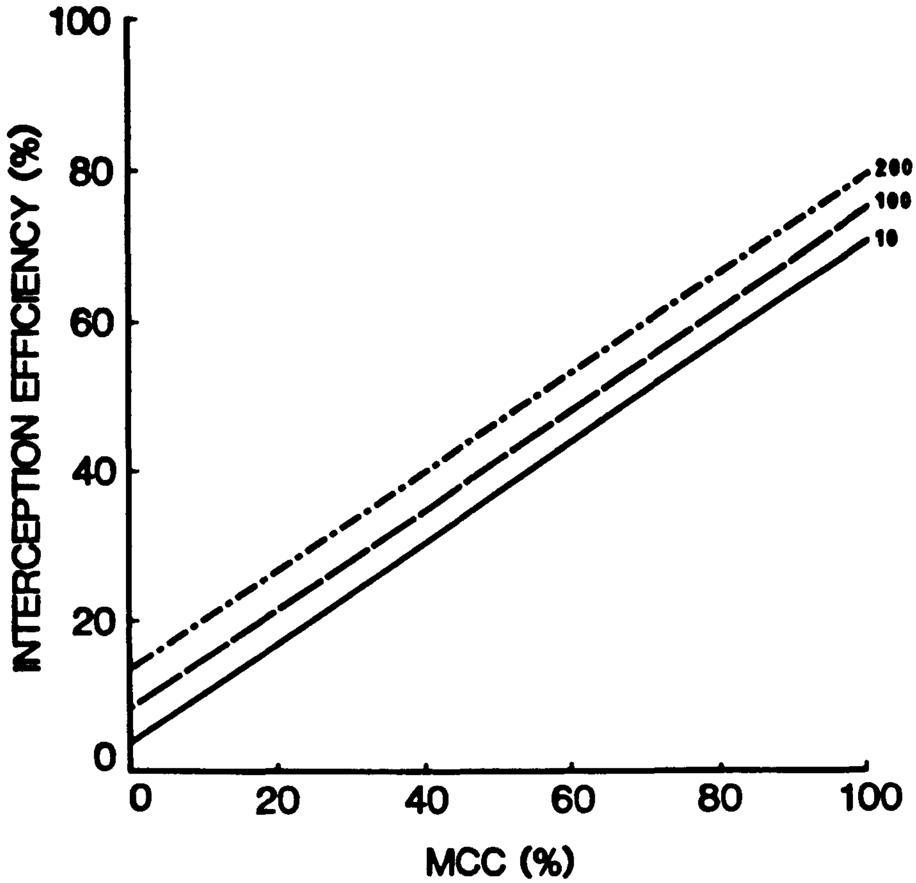


Figure 25. Snow interception efficiency as a function of mean crown completeness where crown surface area classes are (———) 10 m^2, (— — —) 100 m^2, and (—·—) 200 m^2.

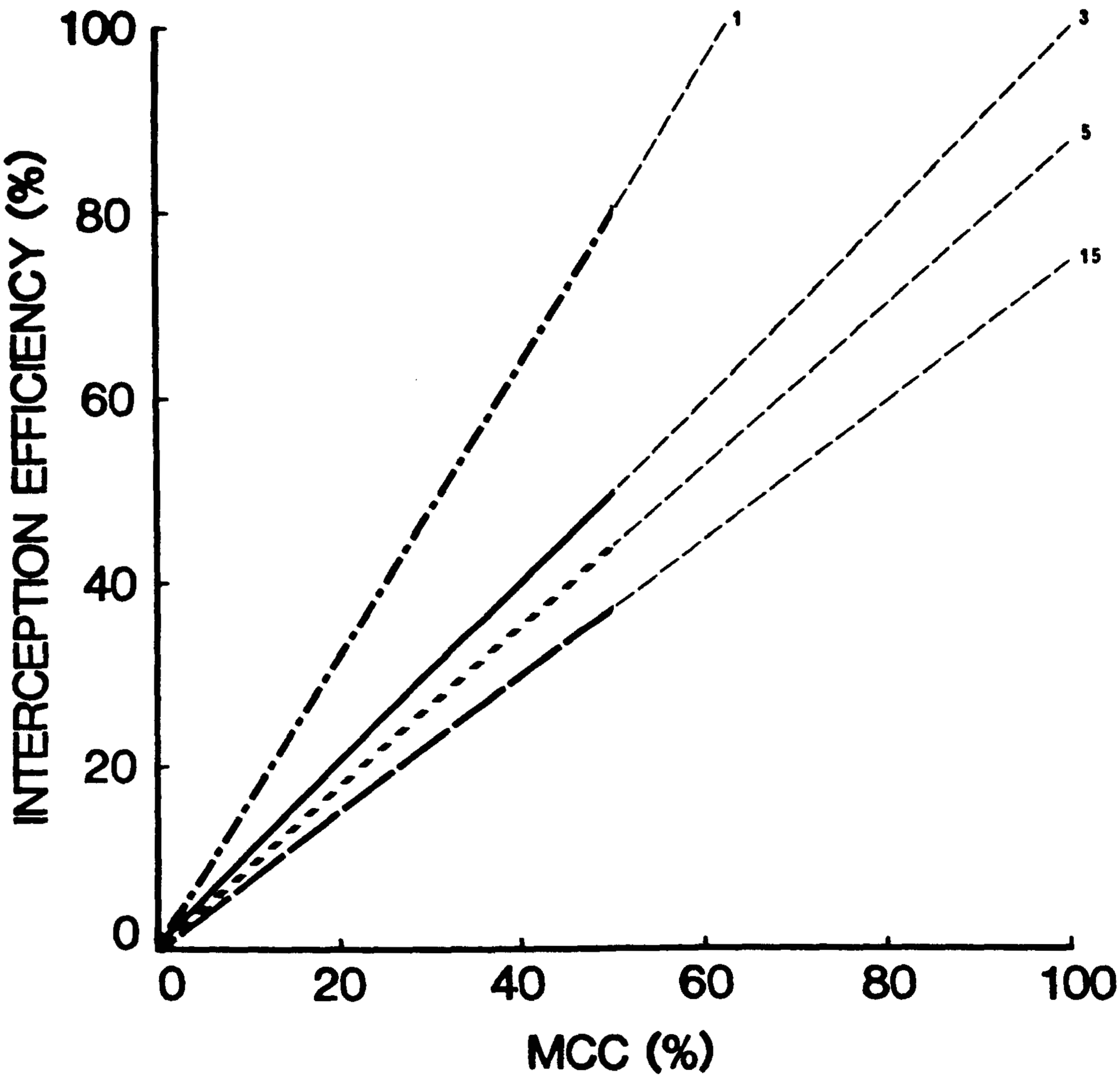


Figure 26. Snow interception efficiency as a function of mean crown completeness where individual storm sizes are (—·—) 1 cm SWE, (——) 3 cm SWE, (- - - -) 5 cm SWE, and (— —) 15 cm SWE.

to young animals (where footloading is approximately 256 g/cm^2) and was derived from data of Bunnell et al. (1985). That study was strictly a sampling project aimed at the preliminary investigation of relationships between deer sinking depth and snowpack attributes. Deer sinking depth was related to snow density and snow surface hardness. While the equation operates well for the empirical situation in which it was developed (1 fawn and in mountainous terrain influenced by a maritime climate), it differs from Parker et al. (1984). In Parker's study, deer always sank to the ground (25-95% of chest height) in snow densities of 0.2 to 0.4 g/cm^3 and snow depths of $\leq$ 60 cm (pers. comm. K. Parker; October 1984). In comparison, the fawn, used for the study by Bunnell et al. (1985), sank only 0-48% chest height in open conditions with an average snow density of 0.39 g/cm^3 and snow depth in excess of 1 metre (see Table 2 in appendix I, II and Fig. 27).

The difference in sinking depth can be attributed partly to higher footloading (350-400 g/cm^2) of the adult deer used by Parker et al. (1984). Furthermore, it is expected that some of the difference was due to a different hardness (g/cm^2).

Relative Energy Expenditure.--The mathematical formulation (Table 2, Appendix I, II) for relative energy expenditure by deer during locomotion in snow was adopted from Parker et al. (1984). The cost of locomotion in snow is expressed as a percentage over the cost of locomotion without snow and is a function of relative sinking depth (RSD) amd snow density.

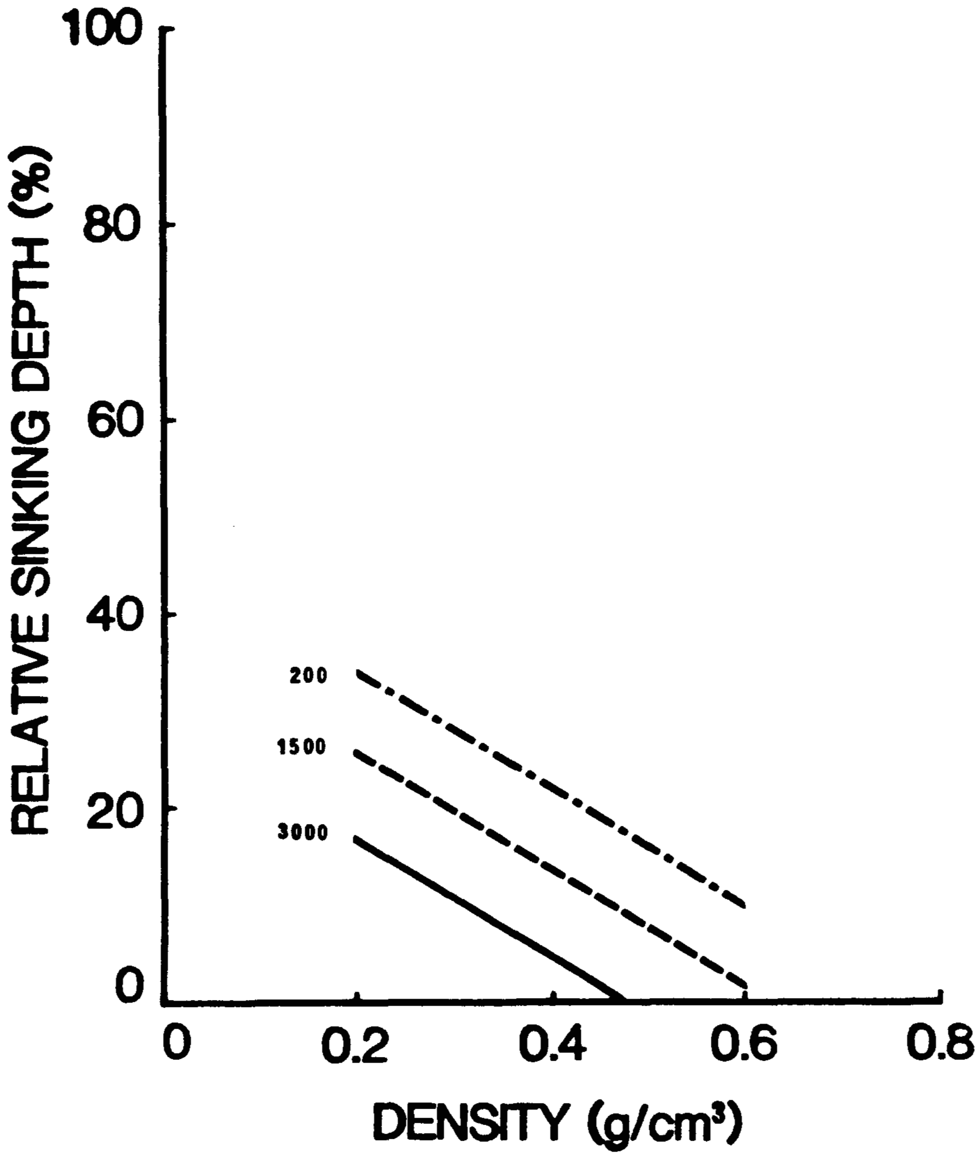


Figure 27. Relative sinking depth of deer as a function of snow density where snow hardness is (—·—) 200 g/cm², (– – –) 1500 g/cm², or (———) 3000 g/cm².

Walking at a velocity of 30 m/min the 36 kg deer used by Bunnell et al. (1985) would use 1.26 kcal/min in no snow and on level terrain (Parker et al. 1984). This base rate would be increased by approximately 200% if, during locomotion in snow, the animal sank up to 50% of its chest height (Fig. 28).

Results.--With snow conditions of 250 g/cm^2 hardness and 0.3 g/cm^3 density, all the models predict that a black-tailed deer fawn will sink 34% of its chest height (Fig. 27). This sinking depth represents a 48% increase in the energy cost for locomotion (Fig. 28). The cost of locomotion remains constant whenever the interception subroutine allows snow depths to accumulate that are $\geq$ 34% chest height (see Figs. 29, 30, and 32).

Young stands, with tree crown surface areas of 10 m^2, cannot intercept enough of a 50 cm snowfall to provide a potential reduction in energy cost to deer. With a crown surface area of 200 m^2, enough snow can be intercepted to reduce locomotion costs when MCC approximates 90% (Fig. 29).

The apparent influence of crown surface area becomes less at lower snowfall intensities (Fig. 29). MCC, however, is more important during snowfalls of less than 50 cm. A snowfall of 10 cm would represent an 64% increase in cost of locomotion to a fawn in open habitat compared with fawns utilizing forests with 80% MCC. The beneficial effect of MCC decreases as snowfall intensity increases but a unit increase in MCC becomes more important. However, the relative increase in cost of locomotion

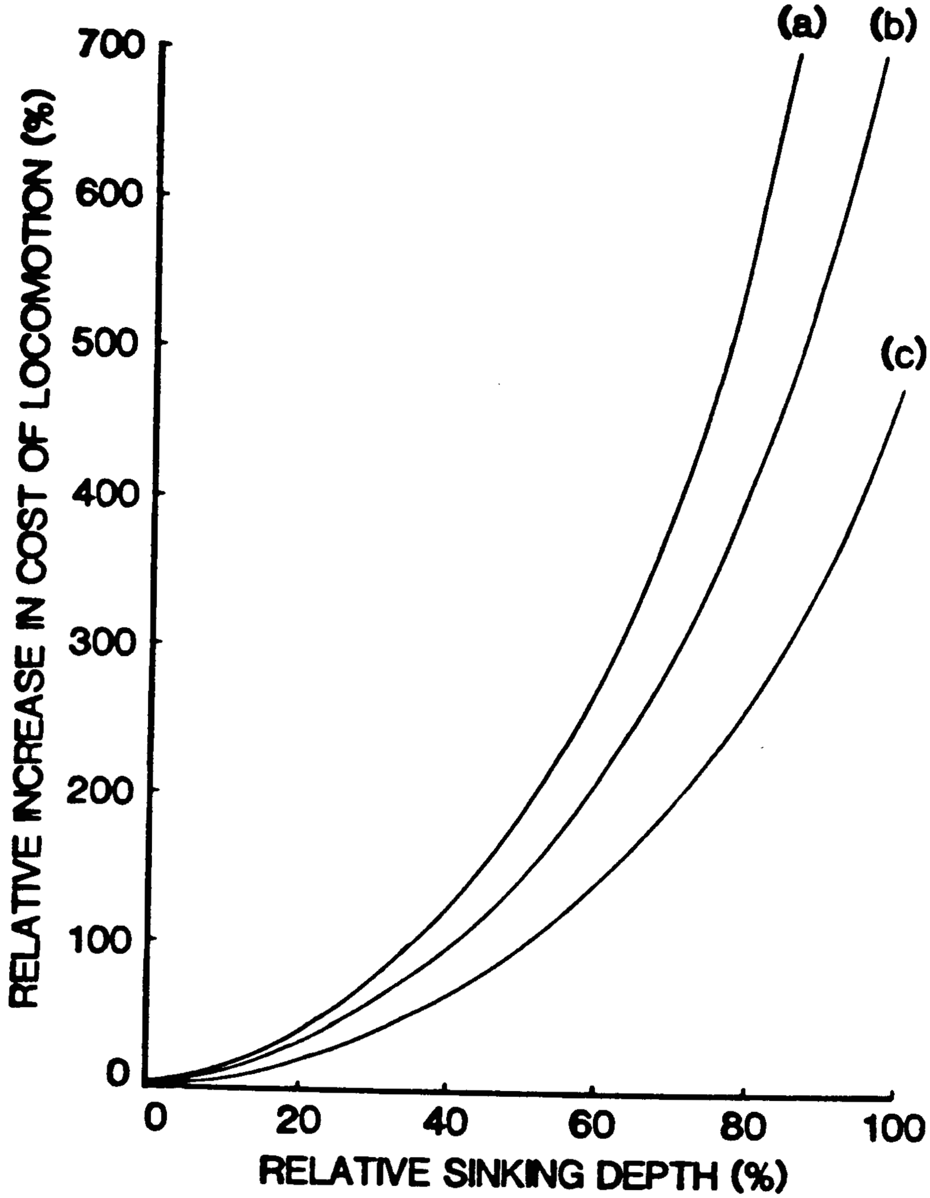


Figure 28. The relative increase in cost of locomotion expressed as a function of relative sinking depth (sinking depth/chest height X 100) where density of snow is (a) 0.20 g/cm^3, (b) 0.30 g/cm^3, and (c) 0.40 g/cm^3 (calculated from Parker et al. 1984: 482).

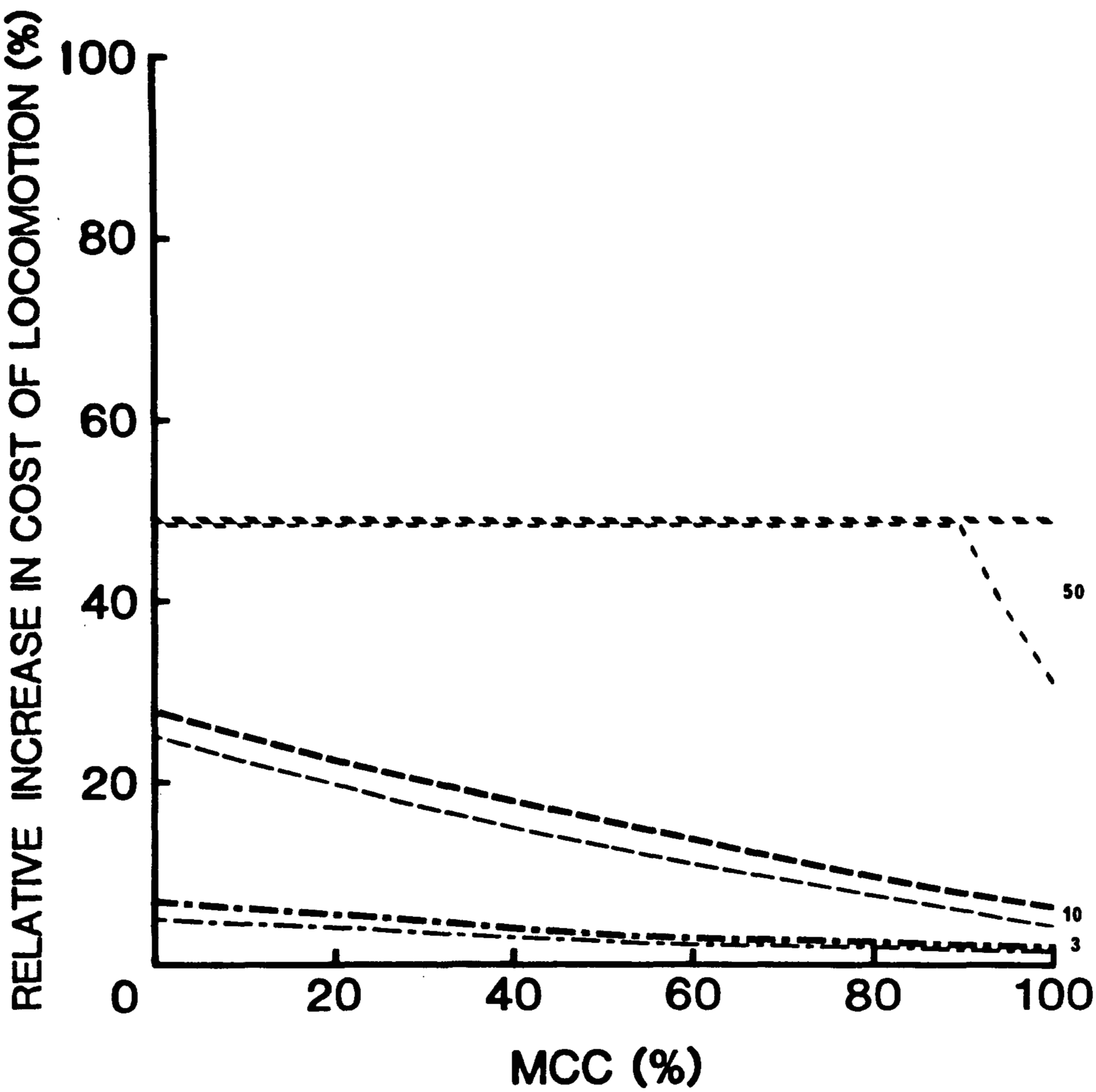


Figure 29. Model IDEPTH - Relative increase in the cost of locomotion for deer as a function of the snow interception by forest MCC where individual snow storm sizes are (—•—) 3 cm, (— — —) 10 cm, and (- - -) 50 cm. Thick lines represent crown surface areas of $50m^2$ whereas thin lines represent a crown surface area of $200m^2$.

decreases as well.

The same generalities are predicted by the ISWE model (Fig. 30). The relative cost of locomotion tends to be higher under comparable snow storm conditions. The discrepancy can be explained in part by the linear influence of storm size in IDEPTH's interception subroutine. Larger storms are intercepted less efficiently in ISWE causing the relative cost of locomotion to be higher than would be predicted by the IDEPTH model.

After a snowfall of 3 cm SWE (roughly equivalent to the 10 cm snowfall discussed for the IDEPTH model), a fawn would be expected to expend 85% more energy in an open habitat as under a forest with MCC equal to 80%. Once again the importance of a given MCC decreases as snowfall intensity increases but a unit increase is more important.

4.2.2 "Snowpack" Interception Model

Fitzharris (1975) reported that snow density is predictable and variations are least during times of maximum snowpack accumulation which is the time during which input data should be collected for the SSWE (Snowpack SWE) model.

The transformation from cm SWE to cm of snow should be more predictive than in the ISWE model simply because the average density estimate is more predictive.

The SSWE is more general than those models based on individual storms and thus should be more useful for general

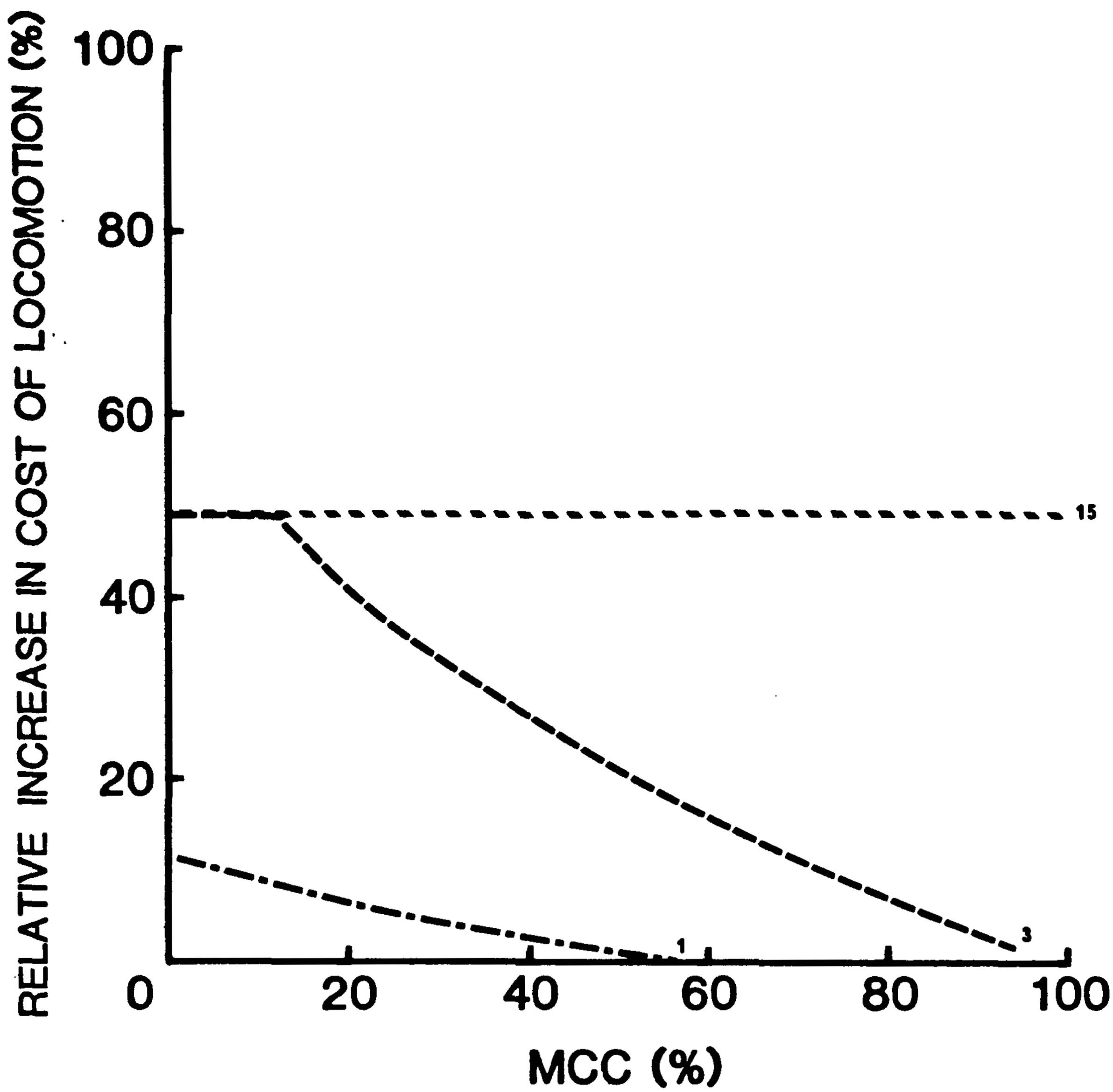


Figure 30. Model ISWE - Relative increase in the cost of locomotion for deer as a function of the snow interception by forest MCC where individual snow storm sizes are (— - —) 1 cm SWE, (— — —) 3 cm SWE, and (- + - -) 15 cm SWE.

management guidelines.

Interception.--The interception subroutine for the SSWE model derives from Equation 16. Storm size influences are taken into account and interstorm melt periods become implicitly incorporated (see Section 4.1.2). According to ISWE a 100% MCC will only intercept 85% of a 5 cm SWE snowfall (Fig. 26). In regions where 5 cm SWE snowpacks accumulate, a 40% MCC will intercept 100% of the snow (Fig. 31). That implies that the remaining 15% of each 5 cm SWE snowfall in the ISWE would eventually melt and would not add to any snowpack accumulation. The process, particularly in maritime climates, is plausible, but the magnitude presented here as an example is untested. The model SSWE indicates that 100% of annual snow accumulations up to 30 cm SWE could potentially be intercepted by forest crowns (Fig. 31).

Deer Sinking Depth And Relative Energy Expenditure.--The SSWE model utilizes the same sinking depth and energy expenditure routines as described for the IDEPTH and ISWE models above.

Results.--The SSWE model indicates that no forest canopy can intercept enough snow to help deer limit the increase in relative cost of locomotion (RCL) in regions where snow annually accumulates to 45 cm SWE (Fig. 32). In regions where snow can accumulate to 30 cm SWE, forest MCC would have to be close to 92% before any reduction in RCL could be realized by deer. An 11% increase in MCC (from 70 to 81%) can cause a 98% reduction

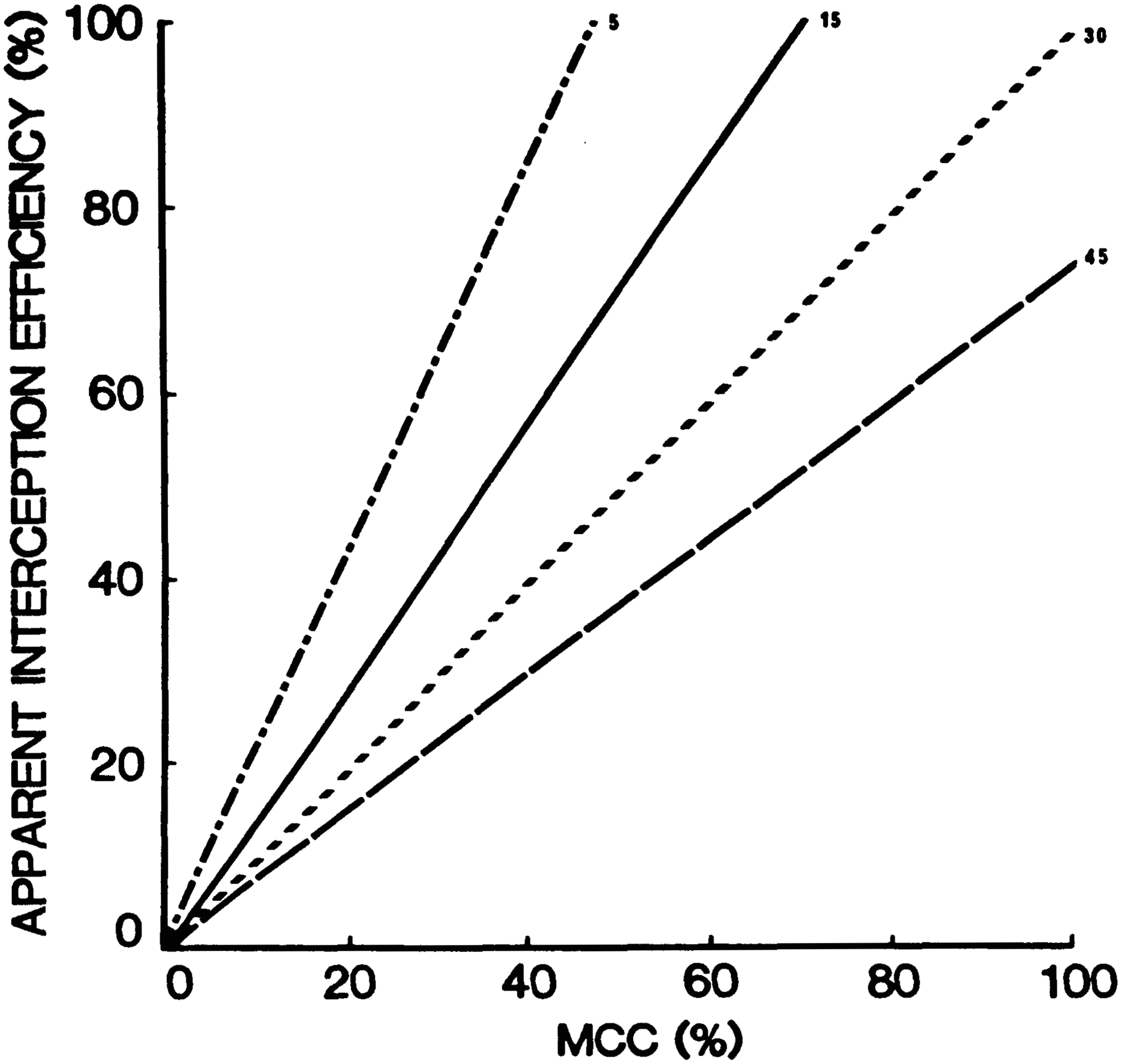


Figure 31. Apparent snow interception efficiency as a function of mean crown completeness where annual SWE accumulations are (-·-·-) 5 cm, (——) 15 cm, (- - -) 30 cm, and (— —) 45 cm.

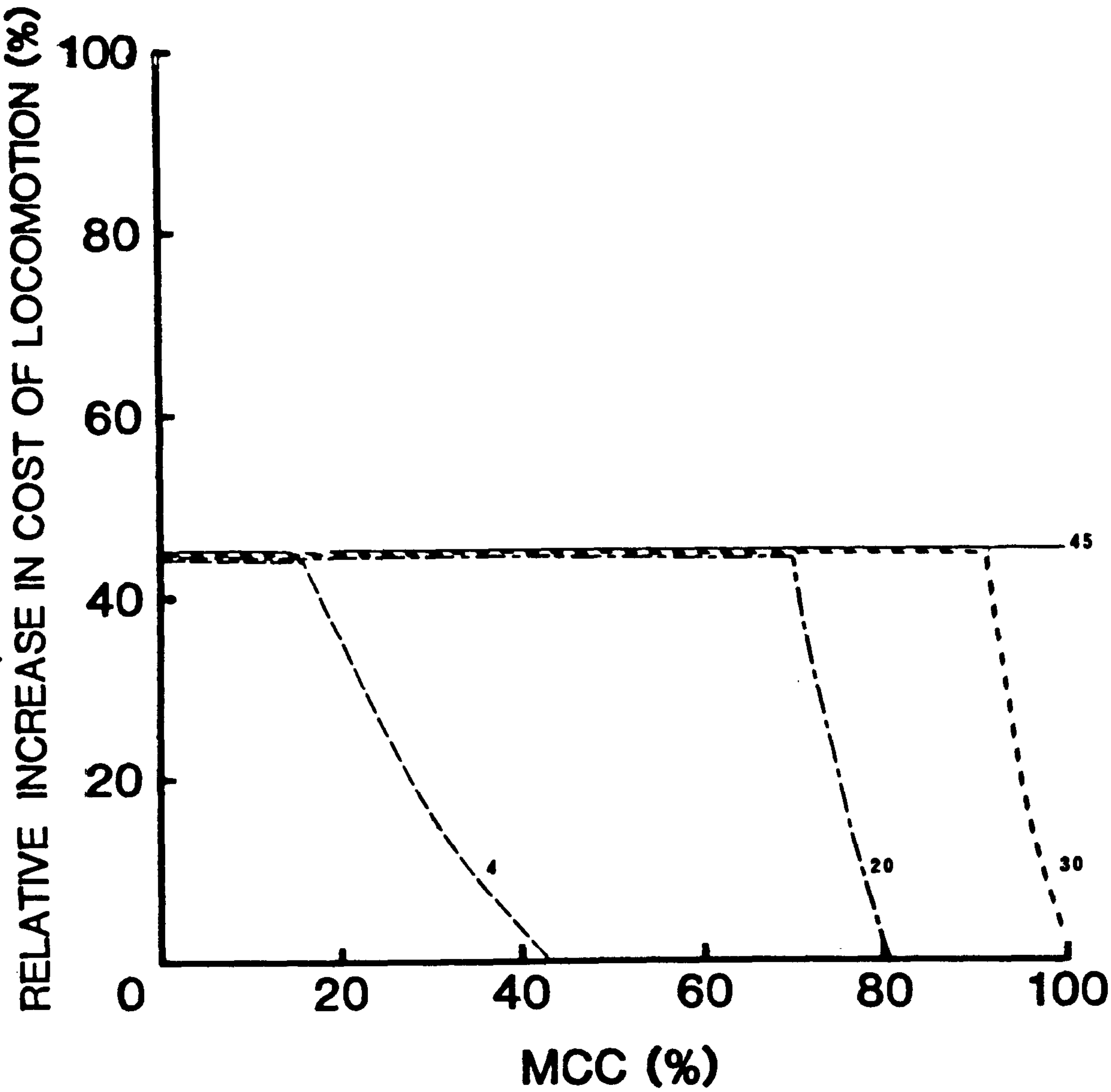


Figure 32. Model SSWE - Relative increase in the cost of locomotion for deer as a function of the snow interception by forest MCC where annual snowpack accumulations are (———) 4 cm SWE, (—-—) 20 cm SWE, (- - - -) 30 cm SWE, and (———) 45 cm SWE.

in RCL where a 20 cm SWE snowpack exists in the open. The same reduction in RCL requires a change in MCC from 16% to 44% in regions where only 4 cm SWE accumulates annually (Fig. 32).

4.2.3 General Conclusions

Generally, the processes governing snow interception by forest stands appear to be applicable to coastal forest climatic and silvicultural conditions. Melt is considered to be a more significant force in creating particular snowpack accumulation (see Section 4.1.1) in coastal environments than in continental regions.

Measurement Of Forest Crown Completeness.--The moosehorn was found to be the best predictor of mean crown completeness (for purposes of predicting snow interception) when compared with the light meter, spherical densiometer, ocular estimates, and photographic estimates utilizing subtended angles of 10°, 20°, and 30°. The angle of the measurement technique and the height to the base of live crown are confounding factors in measuring MCC. These two confounding factors require further study to evaluate their effect and so that recommendations can be made as to the best method to use in particular forest types.

Intra-stand Variability.--Wallmo and Schoen (1980) first identified the spatial heterogeneity of snow depths in old-growth forests. Results here indicate that snowpack depths as well as "new snow" accumulations reflect the canopy heterogeneity of forests. Old-growth forests tend to be more heterogeneous than 50-80 year old second-growth forests (Figure 15). The spatial heterogeneity of old-growth is suspected of being a key feature representing that forest type as high quality deer winter range.

Prediction Of Snow Interception By Forest Canopies.--On an individual storm basis, interception is weakly but significantly related to crown completeness. Second-growth stands, because of their more complete crowns, consistently intercepted more snow than old-growth forests. Interception increases with storm size and there is evidence to suggest this is an asymptotic relationship. Because of the confounding of temperature, the new snow data did not show decreasing IE with increasing storm size, however, snowpack data did confirm this latter relationship.

Results here, although tentative (see Section 4.2.1 and 4.2.2), indicate that canopy manipulations for the purpose of altering the interceptive ability of forest stands should centre around increasing crown surface area and increasing canopy completeness. If wildlife habitat is to be generated simultaneously, then canopy closure should tend toward some compromise that allows sufficient snow interception (i.e., snow accumulations < 50 cm) while maintaining forage production. Spatial pattern of the compromise matrix is expected to be important.

Forest Canopy And Cost Of Locomotion For Deer.--The current models have many weaknesses. They all rely on empirical relationships and are untested. They integrate many site variables and local topographical features and therefore are expected to be very limited in application. The models allow questions regarding fresh, undisturbed snowpacks that exist at discrete points in time. Snow depth, density, and hardness are only three features of snowpacks that describe winter severity to deer; snowpack duration and the temporal and spatial variation of accumulation patterns are two other important aspects of winter severity (Wallmo and Schoen 1980, Verme and Ozoga 1981) that are not incorporated into the models and not expressed in their output. Further, the models imply no behavioural response on the behalf of deer to limit costs of locomotion such as waiting for snowpack conditions to ameliorate or walking on trails (Verme 1968). The individual storm models are less complete than the snowpack model. IDEPTH and ISWE both do not incorporate melt, IDEPTH has no proper storm size function, and ISWE has no proper MCC function.

Nevertheless, in terms of management, the models allow some indication of the effects of crown completeness on costs of locomotion for black-tailed deer fawns. Both models that operate on an individual storm basis show that following a 10 cm snowfall a forest stand with 80% MCC can mean an 85% reduction in energy expenditure for deer compared with open habitat. A higher MCC is required to intercept the same amount of snow at higher snowfall intensities. Unit increases in MCC at high snowfall intensities are more significant than at low snowfall intensities. Therefore, in regions where storms are frequently associated with high snowfall, unit increases in MCC are expected to be more efficient management recommendations than in regions where snowfalls are usually only light.

SSWE is probably the best model to assist in the preparation of management guidelines because it is general and incorporates both melt and storm size as well as the influence of canopy completeness. In regions where snowpacks traditionally accumulates to > 30 cm SWE, MCC manipulations for the management of winter habitat for deer are not expected to yield significant results. Similar to IDEPTH and ISWE, SSWE predicts that a unit increase in MCC is more important in regions where snow accumulates to 20 cm SWE than in regions where only 4 cm SWE accumulates. Management of deer winter habitat is expected to be most efficient where annual snowpacks accumulate to 10-30 cm SWE.

4.3 Future Research

Comparing the snow interception models suggests where future research should be concentrated. Individual storm data provide a process level understanding of why a forest stand may be beneficial for deer. One result is that management guidelines can be precise. General snowpack data provide a knowledge of which forest stands are beneficial to deer. The management guidelines tend to be broader but clearer and simpler than process level information.

If managers need to know why one forest stand is better than another, then research effort should be spent in improving the process level models. This report indicates it would be proper to continue using MCC as the primary independent variable but that snow melt should receive more attention, especially in maritime climates. Because crown closure is the more routine measurement of forest crowns for management purposes, then the relation between MCC and crown closure should be investigated. It would be beneficial to evaluate SCSA as a dependent variable in canopy-snow interception regression equations. Individual storm models may have better application in coastal, B.C. because of the temporal variance associated with snowfall and snowpack accumulation and ablation patterns.

If managers only need to know general prescriptions for future stands that will improve those stands for wildlife then SSWE could be used. Interception of snow by forest stands depends on MCC but it can also be dependent largely on climatic factors such as storm size and inter-storm melt periods. SSWE incorporates these effects implicitly. The future research required for the model SSWE would only be to test and verify its predictions. Managers would subsequently need to stratify areas of application by broad zones of S(o) which implies that some inventory method for S(o) be developed.

If managers use the information provided by the snow interception models (regardless which model) to gain knowledge on the costs of locomotion for deer, then considerable research is required. The new research will have to centre around the issues of deer behaviour and climatic influences, over which managers have little control.

Specific issues are to investigate: 1) deer sinking depths as a function of snowpack characteristics, 2) the influence of behavioural responses (e.g., trailing behaviour, linear distance of travel) on energy expenditure and, 3) the implications of the timing and duration of snowpack accumulation and ablation on the seasonal energy expenditure by deer.

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APPENDIX I

Individual storm - snow interception models

MODEL: IDEPTH ISWE

Two, snow interception - deer energetics models, were developed which pertain to input data on snow characteristics from individual snow storms. One model accepts input in the form of storm specific snowfalls recorded in cm of depth (IDEPTH) and the other accepts data of storm specific snowfalls recorded in cm of snow water equivalent (ISWE).

Both models simulate snow interception over a range of mean canopy completeness from 0-100%. Only ISWE functionally relates storm size to interception efficiency. The simulation procedure is depicted in Figure 1. Table 1 lists the variables conceptualized as being the major contributors to the functional relationships used in the models. The table is presented to indicate which variables have received study and where significant ($P \leq 0.0001$) relationships have been found. The general relationships used in the models are listed in Table 2 along with their attained significance level, coefficients of determination, standard error of estimates, and sample size.

Computer program listings are provided for IDEPTH in Figure 2 and for ISWE in Figure 3.

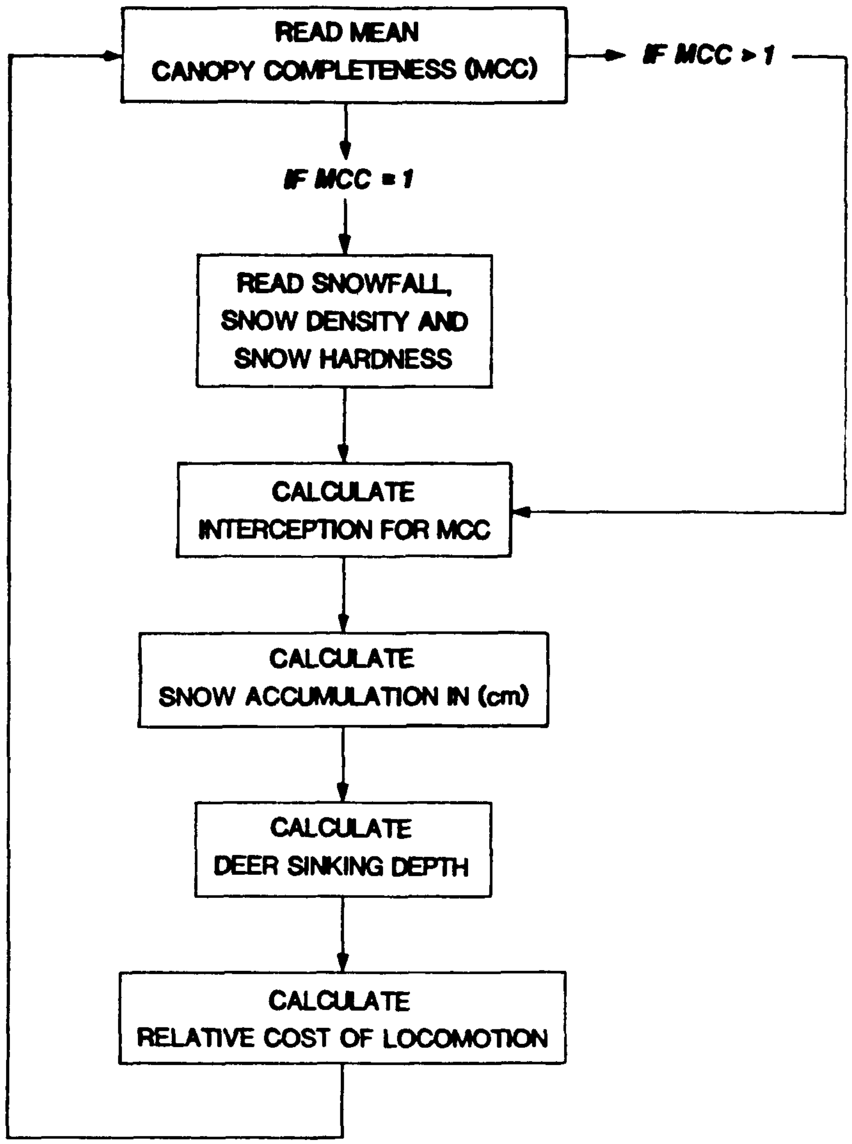

Figure 1. Flow chart for the IDEPTH and ISWE model simulation procedure.

Table 1. Interaction matrix for IDEPTH and ISWE models. Row factors exert a proximal effect on column factors where an (X) occurs. X indicates the relationship is expressed in the models.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 - Aspect										X										
2 - Slope								X												X
3 - (temperature) elevation						X	X	X		X										
4 - SCSA								X												
5 - MCC								X												
6 - Frequency snowfall								X												
7 - Storm size								X												
8 - Interception														X						
9 - Rain											X	X	X							
10 - Degree days											X									
11 - Melt												X	X	X						
12 - Snow density													X				X	X		X
13 - Snow hardness																	X	X		
14 - Snow depth											X						X	X		
15 - Weight																		X		
16 - Hoof area																		X		
17 - Gait																		X		
18 - Sinking depth																				X
19 - Chest height																				X
20 - Relative cost of locomotion																				

Table 2. General relationships used in the IDEPTH and ISWE models

Relationship	Equation[1]	r^2	SE	n	Sig.	Reference
Snow interception						
IDEPTH	$IE = 3.7 + 0.05\ CSA + 0.66\ MCC$	0.92	4.0	21	0.0001	UBCRF unpublished data
ISWE	$IE = \frac{SFW - SGW}{SFW} * 100 * \frac{MCC}{51}$ where, $SGW = (-4.58 + 0.65 * SFW * 10)/10$	0.78	9.9	380	0.0001	Fitzharris (1975)[2]
SWE to cm depth	$DS = 4.36 + 0.97\ (SGW/DEN)$	0.97	6.78	343	0.0001	Equation 11, this report
Deer sinking depth	$SD = 23.03 - (29.13*DEN) - (0.003*HAR)$	0.86	1.59	40	0.0001	Bunnell *et al.* (1985)
Relative sinking depth	$RSD = \frac{SD}{CH} * 100$	-	-	-	-	
Relative cost of locomotion	$RCL = [0.71 + 2.6(DEN-0.2)]RSD*e^{[0.019+0.016(DEN-0.2)]RSD}$	-	-	-	-	Parker *et al.* (1984)

1/ where IE = interception efficiency (%)
CSA = crown surface area (m^2)
MCC = mean canopy completeness (%)
SFW = snowfall (cm SWE) in open
SGW = accumulated snow (mm SWE)
DS = depth snow (cm)
DEN = density of snow (g/cm^3)
HAR = surface hardness of snowpack (g/cm^2)
SD = sinking depth of deer (cm)
CH = chest height of deer (cm)

2/ Equation is recalculation of Fitzharris' data and appears as Equation 2 in this report.

```
90    REM  SET SIMULATION
91    REM
93    MCC=1
106   REM
107   REM  INPUT PARAMETERS
108   REM
110   INPUT "SNOWFALL DEPTH? ";SF
111   INPUT "SNOW DENSITY? ";DEN
112   INPUT "SNOW HARDNESS? ";HAR
113   INPUT "CROWN AREA? ";CSA
125   REM
126   REM  SET CONSTANTS
127   REM
128   CH=48
135   REM
136   REM  INTERCEPT SNOW
137   REM
140   IE=3.7 + (.05 * CSA) + (.66 * MCC)
141   DS=SF - ((IE/100) * SF)
150   REM
151   REM  MOVE DEER IN SNOW
152   REM
200   SD=23.03 - (29.13 * DEN) - (.003 * HAR)
205   IF SD > DS THEN SD = DS
210   RSD=SD/CH * 100
220   REM
221   REM  CALCULATE ENERGY COST
222   REM
223   IF RSD > 100 THEN RSD = 100
230   E=EXP((.019 + 0.16 * (DEN - .2)) * RSD)
240   RCL=((.71 + 2.6 * (DEN - .2)) * RSD) * E
250   PRINT "RELATIVE COST OF LOCOMOTION= ";RCL
260   PRINT "OCCURS AT MCC= ";MCC
280   MCC=MCC + 1
290   IF MCC <= 100 GOTO 140
```

Figure 2. Computer listing of the model - IDEPTH.

```
84     REM  SET SIMULATION
85     REM
87     MCC=1
88     REM
89     REM INPUT PARAMETERS
95     REM
110    INPUT "SNOWFALL SWE? ";SFW
111    INPUT "SNOWDENSITY? ";DEN
112    INPUT "SNOW HARDNESS? ";HAR
114    REM
115    REM  SET CONSTANTS
116    REM
117    CH=48
135    REM
136    REM  INTERCEPT SNOW
137    REM
140    C=(-4.5859 + (0.647*SFW*10))/10
142    IE=((SFW - C)/SFW) * (100/51) * MCC
143    SGW=SFW - ((IE/100) * SFW)
145    IF SGW => 3.0 GOTO 148
146    DS=1.53 * (SGW/DEN)
147    GOTO 200
148    DS=4.36 + 0.97 * (SGW/DEN)
180    REM
181    REM  MOVE DEER IN SNOW
182    REM
200    SD=23.034 - (29.13 * DEN) - (.003 * HAR)
205    IF SD > DS THEN SD = DS
210    RSD=(SD/CH) * 100
220    IF RSD > 100 THEN RSD = 100
222    REM
223    REM  CALCULATE ENERGY COST
224    REM
230    E=EXP((.019 + .016 * (DEN - .2) * RSD)
240    RCL=(.71 + 2.6 * (DEN - .2)) * RSD * E
250    PRINT "RELATIVE COST OF LOCOMOTION= ";RCL
260    PRINT "OCCURS AT MCC= ";MCC
280    MCC=MCC + 1
290    IF MCC <= 100 GOTO 140
```

Figure 3. Computer listing of the model - ISWE.

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APPENDIX II

Snowpack-interception model

MODEL: SSWE

One snow interception-deer energetics model was developed which pertains to input data on snow characteristics from snowpack measurements taken at the time of maximum annual snow accumulation. Input data is in cm of snow water equivalent (SWE).

The model simulates snow interception over a range of mean canopy completeness from 0-100%. The simulation procedure is depicted in Figure 1. Table 1 lists the variables conceptualized as being the major contributors to the functional relationships used in the models. The table is presented to indicate which variables have received study and where significant ($P \leq 0.0001$) relationships have been found. The general relationships used in the model are listed in Table 2 along with their attained significance levels, coefficients of determination, standard error of estimates, and sample sizes.

A computer listing of SSWE is provided in Figure 2.

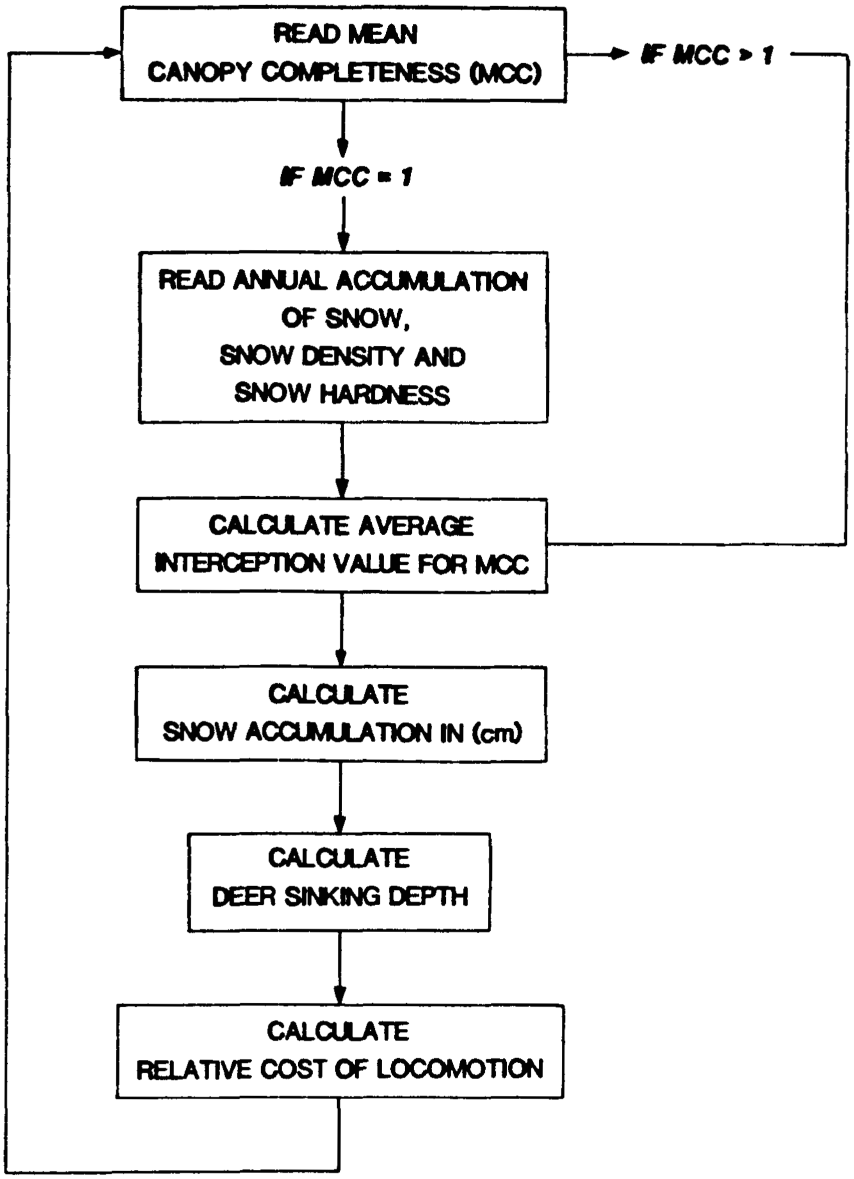

Figure 1. Flow chart for the SSWE model simulation procedure.

Table 1. Interaction matrix for SSWE model. Row factors exert a proximal effect on column factors where an (X) occurs. X indicates that the relationship is expressed in the model.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 - Aspect				X										
2 - Slope					X									X
3 - MCC					X									
4 - SWE pack depth					X									
5 - Interception							X							
6 - Snow density								X			X	X		X
7 - Snow depth						X					X	X		
8 - Snow hardness												X		
9 - Weight												X		
10 - Hoof area												X		
11 - Gait												X		
12 - Sinking depth														X
13 - Chest height														X
14 - Relative cost of locomotion														

Table 2. General relationships used in the SSWE model.

Relationship	Equation[1]	r^2	SE	n	Sig.	Reference
Snow interception	AIE = [SFW-(R/100*SFW)]/SFW*100 where R = 100 + [-3.1 + 0.619* ln (SFW)]*MCC	0.72	0.32	25	0.0000	Bunnell *et al*. (1984)
SWE to cm depth	DS = 4.36 + 0.97 * (SGW/DEN)	0.97	6.78	343	0.0000	Equation 11, this report
Deer sinking depth	SD = 23.03-(29.13*DEN)-(0.003*HAR)	0.86	1.59	40	0.0000	Bunnell *et al*. (1985)
Relative sinking depth	$RSD = \frac{SD}{CH} * 100$	-	-	-	-	
Relative cost of locomotion	$RCL = [0.71 + 2.6\,(DEN-0.2)]RSD * e^{[0.019+0.16(DEN-0.2)]RSD}$	-	-	-	-	Parker *et al*. (1984)

1/ where AIE = apparent interception efficiecy (%)
SFW = snowfall in open (cm SWE)
MCC - mean canopy completeness (%)
SGW = accumulated snow (cm SWE)
SGA = accumulated snow (cm)
DEN = density of snow (g/cm^3)
HAR = surface hardness of snowpack (g/cm^2)
SD = sinking depth of deer (cm)
CH = chest height of deer (cm)

```
91    REM  SET SIMULATION
92    REM
93    MCC=1
94    REM
102   REM  INPUT PARAMETERS
110   REM
111   INPUT "ANNUAL SWE? ";SFW
112   INPUT "AVG. SNOW DENSITY? ";DEN
113   INPUT "SNOW HARDNESS? ";HAR
116   REM
117   REM  SET CONSTANTS
118   REM
119   CH=48
132   REM
133   REM  INTERCEPT SNOW
134   REM
138   A= -3.1 +.617 * LOG(SFW)
139   R=100 + A * MCC
140   IF R < 0 THEN R=0
141   IF R > 100 THEN R=100
143   SGW=(R/100) * SFW
145   IF SGW >= 3.0 GOTO 148
146   DS=1.53 * (SGW/DEN)
147   GOTO 180
148   DS=4.36 + .97 * (SGW/DEN)
150   AIE=((SFW - SGW)/SFW) * 100
173   REM
174   REM  MOVE DEER IN SNOW
175   REM
180   SD=23.034 - (29.13 * DEN) - (.003 * HAR)
206   IF SD > DS THEN SD=DS
210   RSD=SD/CH * 100
220   IF RSD > 100 THEN RSD=100
230   E=EXP((0.19 + .016 * (DEN - .2)) * RSD)
240   RCL=((.71 + 2.6 * (DEN - .2)) * RSD) * E
250   PRINT "RELATIVE COST OF LOCOMOTION= ";RCL
260   PRINT "OCCURS AT MCC= ";MCC
280   MCC=MCC + 1
290   IF MCC <= 100 GOTO 138
```

Figure 2. Computer listing of the model - SSWE.

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